Instytut Dendrologii Polskiej Akademii Nauk

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Wpływ biomasy inwazyjnych drzew na naturalne odnawianie się lasu, różnorodność biologiczną roślinności runa i przyrost biomasy nadziemnej rodzimych drzew

The impact of invasive tree biomass on forest natural regeneration, understory plant biodiversity, and aboveground biomass increments of native trees

Praca doktorska
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Spis treści

Lista publikacji stanowiących rozprawę doktorską

Wyniki badań zostały opublikowane w następujących artykułach naukowych:

1. **Bury S.**, Dyderski M.K. 2024. No effect of invasive tree species on aboveground biomass increments of oaks and pines in temperate forests. Forest Ecosystems 11: 100201. https://doi.org/10.1016/j.fecs.2024.100201
2. **Bury S.**, Dyderski M.K. 2025. Invasive *Prunus serotina* vs. *Robinia pseudoacacia*: How does temperate forest natural regeneration respond to their quantity? NeoBiota 97: 179–213. https://doi.org/10.3897/neobiota.97.135421
3. **Bury S.**, Dyderski M.K. 2025. Invasive *Prunus serotina* and *Robinia pseudoacacia* impact on understory vegetation is species-, habitat-, and season-specific. NeoBiota 100: 207–238. https://doi.org/10.3897/neobiota.100.151606

Abstract

Invasive species are considered one of the greatest threats to native ecosystems. Although they can provide various positive ecosystem services, their impact on biodiversity is often described as negative. Trees, being long-lived and large, can have long-lasting impacts on ecosystems and lead to long-term and extreme changes, for example, in soil chemistry and light conditions. Most current studies focus on comparing invaded forests with non-invaded forests, neglecting the abundance of invasive trees. Biomass, in particular, is rarely used as a quantitative indicator of invasion, and it most accurately reflects the actual amount and the actual impact on modifying environmental conditions and resource usage. The study focused on two North American species: black locust *Robinia pseudoacacia* L. and black cherry *Prunus serotina* Ehrh, and was conducted on 160 study plots in managed forests in western Poland. In addition to differing in the aboveground biomass of invasive species, the plots were also placed in two contexts: habitat context (nutrient-rich habitats with *Quercus robur*/*petraea* and nutrient-poor habitats with *Pinus sylvestris*) and stand age context (middle and close to rotation age). Vegetation surveys were conducted on all 160 plots using the Braun-Blanquet method, and natural regeneration, both seedlings and saplings, was counted. Core samples were collected from *P. sylvestris* and *Quercus* spp. on 72 plots using a Pressler borer, and the relative aboveground biomass increments were calculated at the individual tree and stand levels. It was demonstrated that the aboveground biomass of the invasive species was positively related to the densities of natural regeneration of shrubs and admixture trees, and negatively related to the densities of natural regeneration of the main forest-forming species typical of the studied habitats. Nitrophilous, ruderal, and edge understory plants were associated with the increasing biomass of invasive trees, while acidophilous plants typical of nutrient-poor sites decreased their cover as the aboveground biomass of *P. serotina* and *R. pseudoacacia* increased. We did not demonstrate a significant effect of the proportion of invasive species biomass in the total stand biomass on the relative aboveground biomass increments of *P. sylvestris* and *Quercus* spp. The results obtained as part of the submitted doctoral dissertation are important for the management of *R. pseudoacacia* and *P. serotina* populations in stands dominated by *P. sylvestris* and *Quercus* spp. Neither species studied nor their increasing biomasses should alter the carbon sequestration capacity of *P. sylvestris* and *Quercus* spp. Studies indicate that the most vulnerable to the increasing aboveground biomass of the studied neophytes are

acidophilous species in the understory in nutrient-poor habitats, as well as natural regeneration of the main forest-forming species, i.e., *P. sylvestris* in nutrient-poor forest habitats and *Q. petraea* in nutrient-rich forest habitats. By taking species abundance into account, it is possible to more precisely estimate the balance of gains and losses, as well as economic and ecological gains, and to better plan management and conservation measures.

Streszczenie

Gatunki inwazyjne są jednym z największych zagrożeń dla rodzimych ekosystemów. Pomimo faktu, że mogą spełniać różne pozytywne usługi ekosystemowe to ich wpływ na różnorodność biologiczną jest często określany jako negatywny. Drzewa, jako gatunki długowieczne i osiągające duże rozmiary, mogą prowadzić do długofalowych i ekstremalnych zmian warunków środowiskowych ekosystemów leśnych np. chemizmu gleby, warunków świetlnych. Większość dotychczasowych badań skupiała się na porównaniu drzewostanów zasiedlonych i niezasiedlonych przez gatunki inwazyjne, pomijając obfitość występowania inwazyjnych drzew. Zwłaszcza zastosowanie biomasy jako wskaźnika ilościowego inwazji było bardzo rzadko stosowane, podczas gdy wskaźnik ten najdokładniej odzwierciedla faktyczną ilość gatunku w ekosystemie, a w konsekwencji faktyczny wpływ na modyfikacje warunków środowiskowych i zużycie zasobów. Obiektem badań były dwa północnoamerykańskie gatunki: robinia akacjowa *Robinia pseudoacacia* L. i czeremcha amerykańska *Prunus serotina* Ehrh. Badania przeprowadzono na 160 powierzchniach badawczych w lasach gospodarczych w zachodniej Polsce. Powierzchnie różniły się między sobą biomasą części nadziemnej badanych gatunków inwazyjnych. Dodatkowo badania umieszczono w dwóch kontekstach: siedliskowym (siedliska żyzne z dębem i ubogie z sosną) i wiekowym drzewostanów (drzewostany w wieku średnim i bliskorębnym). Na wszystkich 160 powierzchniach wykonano zdjęcia fitosocjologiczne metodą Braun-Blanqueta oraz policzono odnowienia naturalne — osobno siewki i młode drzewka do 1,3 m wysokości. Na 72 powierzchniach z sosen i dębów pobrano próbki przyrostowe za pomocą świdra Presslera. Na ich podstawie określono względny przyrost biomasy nadziemnej na poziomie pojedynczych drzew i całego drzewostanu. Wykazano, że zależność pomiędzy biomasą gatunku inwazyjnego i zagęszczeniem odnowień naturalnych krzewów oraz drzew domieszkowych była pozytywna, a dla zagęszczeń odnowień głównych gatunków lasotwórczych typowych dla badanych siedlisk – negatywna. Z rosnącą biomasą gatunków inwazyjnych związane było występowanie nitrofilnych, ruderalnych i okrajkowych gatunków roślin runa. Na siedliskach ubogich gatunki acydofilne zmniejszały swoje pokrycia wraz ze wzrostem biomasy nadziemnej robinii akacjowej i czeremchy amerykańskiej. Nie wykazaliśmy istotnego wpływu udziału gatunku inwazyjnego w całkowitej biomasie drzewostanu na względny przyrost biomasy nadziemnej sosen i dębów. Wyniki uzyskane w ramach przedłożonej rozprawy

doktorskiej są istotne dla zarządzania populacjami robinii akacjowej i czeremchy amerykańskiej w drzewostanach zdominowanych przez sosnę zwyczajną i rodzime gatunki dębów. Oba badane gatunki i ich rosnące biomasy nie powinny modyfikować zdolności sekwestracji dwutlenku węgla u rodzimych sosen i dębów. Badania wskazują, że najbardziej narażone na rosnącą biomasę nadziemną badanych neofitów są gatunki acydofilne w runie na siedliskach ubogich oraz odnowienia naturalne głównych gatunków lasotwórczych tj. sosny zwyczajnej na siedlisku boru mieszanego świeżego i dębu bezszypułkowego na siedliskach lasu mieszanego świeżego i lasu świeżego. Dzięki uwzględnieniu ilości gatunku inwazyjnego w ekosystemie możliwe jest bardziej precyzyjne oszacowanie bilansu zysków i strat i zysków ekonomicznych i ekologicznych oraz lepsze planowanie działań gospodarczych i ochronnych.

1. Wstęp

W dobie globalnych zmian środowiskowych, napędzanych działalnością człowieka, w tym zmian klimatu, inwazje biologiczne stają się coraz bardziej powszechne. Inwazyjne gatunki drzew mogą wpływać na różnorodne funkcje ekosystemowe, zarówno pozytywnie jak i negatywnie (Castro-Diez i in., 2019; Milanović i in., 2020). W Europie wiele gatunków drzew obcego pochodzenia było sadzonych w różnych celach np. fitomelioracyjnych, glebochronnych, wodochronnych, biocenotycznych, ozdobnych i produkcyjnych np. jako źródła drewna. Niestety, niektóre introdukowane gatunki bardzo dobrze odnalazły się w nowo zasiedlonych miejscach, zaczęły się z sukcesem rozmnażać i sukcesywnie zwiększały i nadal zwiększają zasięg swojego areału (Muys i in., 1992; Starfinger i in., 2003; Godefroid i in., 2005; Nyssen i in., 2024). Inwazyjne drzewa modyfikują warunki środowiskowe (Richardson i in., 2000; Crooks, 2002; Corenblit i in., 2014; Wohlgemuth i in., 2022; Jagodziński i in., 2024), zmieniają warunki świetlne (Starfinger i in., 2003; Dyderski i Jagodziński, 2019a,b) i obieg pierwiastków chemicznych (Rice i in., 2004; Aerts i in., 2017; Horodecki i Jagodziński, 2017; Wohlgemuth i in., 2022). Negatywną konsekwencją transformacji (*sensu* Richardson i in. 2000) zasiedlanych siedlisk jest utrata różnorodności biologicznej (Parker i in., 1999; Woziwoda i in., 2019; Wohlgemuth i in., 2022; García i in., 2023), wycofywanie się gatunków wyspecjalizowanych (Woziwoda i in., 2019; Bärmann i in., 2023; Bury i Dyderski, 2025a) oraz biotyczna homogenizacja ekosystemów (Trentanovi i in., 2013; Šibíková i in., 2019; Wohlgemuth i in., 2022). W celu ograniczenia negatywnych skutków, inwazyjne drzewa są usuwane np. mechanicznie lub chemicznie. Zabiegi eradykacji inwazyjnych drzew są bardzo czasochłonne, kosztochłonne i nie zawsze obojętne dla środowiska naturalnego. Z usuniętych osobników łatwo odrastają nowe pędy (Starfinger i in., 2003; Vítková i in., 2017; Bouteiller i in., 2023; Nyssen i in., 2024), lub w wyniku powstania luki zwiększają się szanse na to, że więcej siewek szybko zwiększy swoje rozmiary (Closset-Kopp i in., 2007), co prowadzi do nasilenia się inwazji (Namura-Ochalska i Borowa, 2015; Nyssen i Vanhellemont, 2016).

Większość obecnych badań bazuje na porównywaniu drzewostanów zasiedlonych i niezasiedlonych przez gatunki inwazyjne. Bardzo mało prac porusza temat wpływu ilości i obfitości inwazyjnych drzew na poszczególne usługi ekosystemowe (np. Chabrerie i in., 2008; Dickie i in., 2011; Czortek i in., 2023, 2025; García i in., 2023; Wiatrowska i in.,

2023; Jagodziński i in., 2024). Tymczasem wpływ gatunków inwazyjnych na ekosystem można opisać jako iloczyn zajmowanej przez nie powierzchni, zagęszczenia lub biomasy na jednostkę powierzchni, oraz wpływu na jednostkę ilości, czyli efektu *per capita* (Parker i in., 1999; Pearse i in., 2019). Ilość gatunku inwazyjnego w ekosystemie może być opisana na wiele sposobów. Stosunkowo proste w zastosowaniu jest zwarcie koron (wykorzystywane np. przez Chabrerie i in., 2008; Wiatrowską i in., 2023 czy Czortka i in. 2025), gdyż bazuje na szacowaniu, a nie pomiarach dendrometrycznych. Miara ta jest wystarczająca w przypadku układów z drzewostanami jednopiętrowymi i jednowiekowymi, przy podobnych rozmiarach drzew lub krzewów (Bury i Dyderski, 2024). Kolejnym wskaźnikiem ilościowym jest zagęszczenie osobników lub ramet. Miara ta jest również łatwa do zastosowania, nie uwzględnia jednak rozmiarów osobników, podczas gdy drzewa to organizmy które osiągają rozmiary od bardzo małej siewki do osobników bardzo starych, grubych i wysokich. Powszechne w zastosowaniu są też wskaźniki bazujące na pomiarach dendrometrycznych: pole powierzchni przekroju pierśnicowego, miąższość oraz biomasa (Younginger i in., 2017; Bury i in. 2024; Engel i in., 2024).

Obiektem badań są dwa północnoamerykańskie gatunki drzew: robinia akacjowa *Robinia pseudoacacia* L. i czeremcha amerykańska *Prunus serotina* Ehrh. Oba te gatunki wprowadzone były w Europie na początku XVII wieku., a na szeroką skalę zaczęły na masową skalę były sadzone już w XIX wieku (Starfinger i in., 2003; Cierjacks i in., 2013; Engel i in., 2024). Robinia akacjowa to pionierski gatunek drzewa, które dzięki symbiozie z bakteriami nitryfikacyjnymi jest zdolne do wiązania azotu atmosferycznego. Z tego względu może rosnąc na bardzo ubogich glebach, a jej opad materii organicznej mocno zmienia obieg pierwiastków chemicznych (Binkley, 1992; Cierjacks i in., 2013; Kanzler i in., 2021; Slabejová i in., 2023). Robinia akacjowa może mieć formę niskiego drzewa lub krzewu, ale również może występować w drzewostanie jako drzewo górujące, panujące i współpanujące (Cierjacks i in., 2013; Nicolescu i in., 2020; Bury i Dyderski, 2024). Nasiona robinii akacjowej są rozsiewane przez wiatr, lecz wiele z nich opada pod okapem drzew rodzicielskich (Vítková i in., 2017), gatunek ten często rozmnaża się wegetatywnie przez odrosty korzeniowe (Bouteiller i in., 2023). Mają one duże znaczenie, ponieważ ponad 99% siewek które wykiełkowały pod okapem drzewostanu nie przeżywa pierwszego roku (Dyderski i Jagodziński, 2019b). Czeremcha amerykańska to niskie drzewo lub krzew, występujący we wczesnych i przejściowych fazach sukcesji, związane

z obecnością luk w drzewostanach (Starfinger i in., 2003; Godefroid i in., 2005; Closset-Kopp i in., 2007; Engel i in., 2024). Nasiona czeremchy amerykańskiej rozsiewane są głownie przez zwierzęta, lecz większość opada pod okapem owocujących drzew (Starfinger i in., 2003; Deckers i in., 2008; Kurek i in., 2024). Dodatkowo gatunek ten rozmnaża się wegetatywnie przez odrosty korzeniowe (Starfinger i in., 2003; Deckers i in., 2008). W lasach środkowej Europy, opisane gatunki różnią się zatem biologią, preferencjami co warunków siedliskowych, oraz osiągają różne rozmiary (Halarewicz, 2012; Bury i in., 2024; Bury i Dyderski, 2025a,b).

Zarówno robinia akacjowa (391 porównań z gatunkami rodzimymi) jak i czeremcha amerykańska (351 porównań) są dobrze reprezentowane w przeglądzie wpływu neofitów na różnorodność biologiczną i funkcjonowanie gleby w Europie (2276 porównań; Wohlgemuth i in., 2022). Dodatkowo systematyczny przegląd przeprowadzony przez Vilę i in., (2024) potwierdza, że rośliny są najlepiej zbadane wśród wszystkich grup systematycznych pod kątem ich reakcji na obecność roślin inwazyjnych. Dodatkowo, cytowana wyżej autorka potwierdza, że robinia akacjowa i czeremcha amerykańska są jednymi z pięciu najczęściej badanych gatunków inwazyjnych roślin w Europie. Często badacze i badaczki koncentrują się na pojedynczych elementach ekosystemu i pojedynczych usługach ekosystemowych. Holistyczne podejście do badań pozwala na bardziej miarodajną ocenę bilansu strat i zysków związanych z uprawą danych gatunków inwazyjnych (Lazzaro i in., 2018; Stanek i in., 2020). Przyrost biomasy drzew oraz naturalne odnawianie się to kluczowe elementy funkcjonowania lasu, a różnorodność biologiczna roślin runa mówi nam o stanie zdrowotnym i stabilności lasu. Wszystkie te usługi ekosystemowe mogą być modyfikowane przez obecność inwazyjnych drzew (Bury i Dyderski, 2024, 2025a,b,c).

Przyrost biomasy drzew jest w dużej mierze uzależniony od struktury zmieszania gatunków. W ekosystemie leśnym nieustannie zachodzą procesy konkurencji wewnątrz i międzygatunkowej, a współobecność różnych gatunków drzew oparta jest na zasadzie komplementarności wykorzystania zasobów. Poszczególne gatunki często mają różne nisze ekologiczne i różne wymagania środowiskowe, więc ich współobecność może być obustronnie korzystna (Forrester i Bauhus, 2016; Pretzsch i Forrester, 2017; Bury i Dyderski, 2024).

Odnowienie naturalne zapewnia przemianę pokoleń w lasach (Oliver i Larson, 1996; Baraloto i in., 2005; Käber i in., 2023) i jest cenioną alternatywą dla odnowienia sztucznego (Jaworski i in., 2007; Batavia i Nelson, 2016; Palik i D'Amato, 2017). Młode pokolenie pochodzące z naturalnego obsiewu jest lepiej dostosowane do lokalnych warunków (Jaworski i in., 2007; Komisja Europejska, 2023). Co więcej, odnawianie lasu w sposób naturalny jest mniej kosztochłonne niż siew czy sadzenie (Oluwajuwon i in., 2024). W przypadku odnowienia naturalnego pomijamy kosztowny proces produkcji materiału sadzeniowego i nie jest wymagane jego nawożenie i podlewanie.

Różnorodność biologiczna roślinności runa mówi nam o kondycji siedlisk i o warunkach które panują w drzewostanie. Poszczególne siedliska, zbiorowiska leśne charakteryzują się specyficzna pulą gatunków (Matuszkiewicz, 2001; Ellenberg i Leuschner, 2010). W wyniku różnej działalności człowieka (Andersen, 2019; Kutnar i in., 2019), w tym inwazji biologicznych (np. Chabrerie i in., 200; García i in., 2023; Jagodziński i in., 2024; Petri i Ibáñez, 2024) warunki środowiskowe mogą być przekształcane i skutkuje to zmianami w składach gatunkowych zbiorowisk. Dodatkowo skład gatunkowy roślinności jest uzależniony od pory roku (Rautiainen i in., 2011; Rawlik i in., 2023). W grądach różnice między sezonami są zaznaczone mocniej: wiosną dominują tam geofity, a latem rośliny cienioznośne i trwałe byliny, co jest związane z dynamiką rozwoju liście drzew (Heinrich, 1976; Kudo i in., 2008; Heberling i in., 2019; Rawlik i in., 2023).

Zarządzanie inwazyjnymi drzewami powinno być dostosowane do biologii i ekologii gatunków, z uwzględnieniem cech takich jak dynamika wzrostu, konkurencyjność czy sposób dyspersji nasion. Bardzo istotny jest również kontekst siedliskowy, gdyż nie każde siedliska są tak samo odporne na transformacje i negatywne oddziaływanie inwazyjnych drzew. Wszelakie zabiegi związane z usuwaniem inwazyjnych drzew lub ich integracja z lasem powinny być dostosowane do aktualnie panujących tam warunków tj. składu gatunkowego roślinności runa, podszytu i drzewostanu, obfitości inwazyjnych drzew, oraz warunków panujących w drzewostanie (Nyssen i Vanhellemont, 2016; Sádlo i in., 2017; Engel i in., 2024; Nyssen i in., 2024). Wyniki uzyskane przy realizacji rozprawy doktorskiej powinny dostarczyć nowych informacji na temat konsekwencji obecności robinii akacjowej i czeremchy amerykańskiej w lasach środkowoeuropejskich, które będzie można wykorzystać w ulepszeniu dotychczasowego zarządzania populacjami tych gatunków.

2. Cel i hipotezy

Celem rozprawy doktorskiej jest zbadanie wpływu ilości gatunku inwazyjnego w ekosystemie, wyrażonego biomasą części nadziemnej drzew na (1) przyrost biomasy części nadziemnej sosen zwyczajnych i dębów szypułkowych/bezszypułkowych, (2) zagęszczenie i skład gatunkowy odnowień naturalnych, (3) różnorodność biologiczną i skład gatunkowy roślin naczyniowych runa leśnego.

Postawiono następujące hipotezy badawcze:

H1: Robinia akacjowa i czeremcha amerykańska w różny sposób wpłyną na przyrost biomasy nadziemnej sosen i dębów. Relacja biomasy inwazyjnych drzew i przyrostu biomasy nadziemnej rodzimych drzew będzie oparta na równoważeniu się dwóch zjawisk – konkurencji i wspomagania (Forrester i Bauhus, 2016). Robinia akacjowa często występuje w głównym piętrze drzewostanu, zmieniając warunki świetlne (Dyderski i Jagodziński, 2019a; Slabejová i in., 2023), wodne i glebowe (Cierjacks i in., 2013; Vítková i in., 2017), w różny sposób na siedliskach ubogich, zdominowanych przez sosnę i na siedliskach żyznych zdominowanych przez dęby, z kolei robinie akacjowe i czeremchy amerykańskie występujące w podszycie będą wpływać na rodzime drzewa głownie pośrednio przez zmianę warunków glebowych i wodnych.

H2: Zwiększająca się biomasa robinii akacjowej w drzewostanach sosnowych spowoduje zmniejszanie się zagęszczeń odnowień gatunków preferujących niższe pH gleby i zwiększenie się udziału gatunków nitrofilnych i preferujących gleby o wyższym pH. Zwiększająca się biomasa czeremchy amerykańskiej spowoduje wycofywanie się gatunków światłożądnych i promowanie gatunków cienioznośnych. Na żyznych siedliskach z dębem zaobserwujemy zwiększenie się różnorodności gatunkowej odnowień naturalnych. Gatunki inwazyjne zwiększą zagęszczenia pozostałych gatunków obcego pochodzenia doprowadzając do zjawiska zwanego „*invasional meltdown*" (Simberloff i Holle, 1999; Ricciardi i Simberloff, 2025). Według tej hipotezy obecność jednego lub więcej gatunków inwazyjnych ułatwia pojawianie się i rozprzestrzenianie się nowych gatunków obcego pochodzenia, nasilając w ten sposób destabilizację ekosystemu.

H3: Związek biomasy czeremchy amerykańskiej i robinii akacjowej z różnorodnością biologiczną roślin naczyniowych runa będzie specyficzny dla gatunku inwazyjnego drzewa, gatunku rośliny runa, siedliska i pory roku. Badane inwazyjne drzewa w różny sposób wpływają na transformacje (Richardson i in., 2000) warunków środowiskowych co będzie z jednej strony promowało, a z drugiej ograniczało występowanie poszczególnych gatunków roślin runa (Chabrerie i in., 2010; Woziwoda i in., 2019). Najbardziej narażone będą gatunki typowe dla borów sosnowych (Halarewicz i Pruchniewicz, 2015; Woziwoda i in., 2019; Dyderski i Jagodziński, 2020). Rośliny aspektu wiosennego będą mniej wrażliwe na zwiększającą się biomasę robinii akacjowej i czeremchy amerykańskiej niż gatunki pełni lata, ze względu na szczyt ich rozwoju przed pełnym ulistnieniem drzew (Heinrich, 1976; Rawlik i in., 2023).

3. Materiały i metody

3.1. Teren badań i badane siedliska

Badania przeprowadzono w lasach gospodarczych w zachodniej Polsce na terenie pięciu nadleśnictw Regionalnej Dyrekcji Lasów Państwowych w Poznaniu: Babki, Konstantynowo, Łopuchówko, Czerniejewo, Jarocin. Teren badań objął dwie jednostki geograficzne: Nizinę Południowowielkopolską i Pojezierze Wielkopolskie. Obie te krainy znajdują się w zasięgu strefy klimatu umiarkowanego przejściowego ze średnią roczną temperaturą wynoszącą 8,5°C i roczną sumą opadów wynoszącą 500-550 mm (BDL, 2025).

Powierzchnie badawcze założono na dwóch typach siedlisk leśnych: ubogich w składniki odżywcze borach zdominowanych przez sosnę zwyczajną i na siedliskach żyznych zdominowanych przez rodzime dęby (szypułkowego i bezszypułkowego). Siedliska ubogie reprezentowały zespół suboceanicznego boru sosnowego *Leucobryo-Pinetum* W. Mat. (1962) 1973, miejscami przechodzące w kierunku *Querco roboris-Pinetum* Mat. et Polak. 1955 s.l. oraz leśne zbiorowiska zastępcze z sosną zwyczajną. Siedliska żyzne reprezentował zespół grądu środkowoeuropejskiego *Galio sylvatici-Carpinetum* Oberd. 1957 i leśne zbiorowiska zastępcze z dominacją dębów na siedliskach grądowych. W ujęciu typologicznym siedliska ubogie były tożsame z borem mieszanym świeżym a siedliska lasowe z lasem mieszanym świeżym i lasem świeżym.

3.2. Układ badań

Założono 160 powierzchni badawczych w kształcie koła o powierzchni 500 m^2 (r= 12,62 m). Wszystkie powierzchnie założono w lasach gospodarczych, unikając drzewostanów w których w ostatnich kilku latach były wykonywane zabiegi gospodarcze. Wyszukiwano powierzchnie w wariantach uwzględniających: gatunek inwazyjnego drzewa (powierzchnie z robinią akacjową i czeremchą amerykańską), typ siedliska (ubogie w składniki odżywcze zdominowane przez sosnę zwyczajną; bogate w składniki odżywcze zdominowane przez dęba bezszypułkowego/szypułkowego), poziom inwazji (kontrolne – 0 %; ze średnim pokryciem – do 30 %; z dużym pokryciem – ponad 50 %), wiek drzewostanu (średni – 40-60 lat; bliskorębny – 80-100 lat dla sosen i 100-140 lat dla dębów). Pokrycie gatunku inwazyjnego było wykorzystane wyłącznie jako miara pomocnicza, do określenia gradientu inwazji wykorzystano dokładniejsze pomiary (zob. 3.3.). Minimalna odległość pomiędzy powierzchniami z poszczególnych wariantów wynosiła 5 km, aby uniknąć autokorelacji przestrzennej.

3.3. Gradient ilościowy inwazji

Na każdej powierzchni badawczej wykonałem pomiary struktur drzewostanów. Zmierzono pierśnice 22101 drzew i krzewów reprezentujących 59 gatunków. Na podstawie pomierzonych pierśnic obliczono biomasy nadziemne poszczególnych drzew stosując opublikowane modele allometryczne (Brown, 1976; Alberti i in., 2005; Forrester i in., 2017; Zasada, 2017; Jagodziński i in., 2018, 2019a). Robinia akacjowa i czeremcha amerykańska osiągnęły różne zakresy biomasy części nadziemnej. Biomasa nadziemna czeremchy amerykańskiej wynosiła od 0,18 do 47,11 Mg ha^{-1} (ze średnią ± SE 7,34 ± 8,75 Mg ha^{-1}) na siedliskach borowych i od 0,19 do 27,39 Mg ha^{-1} (6,68 ± 7,24 Mg ha^{-1}) na siedliskach lasowych. Biomasa nadziemna robinii akacjowej wynosiła od 0,22 do 153,00 Mg ha^{-1} (20,91 ± 31,69 Mg ha^{-1}) na siedliskach borowych i od 0,82 do 278,24 Mg ha^{-1} (50,77 ± 70,37 Mg ha^{-1}) na siedliskach lasowych.

3.4. Przyrost biomasy nadziemnej sosen i dębów

PUBLIKACJA 1: *No effect of invasive tree species on aboveground biomass increments of oaks and pines in temperate forests.*

Na 72 powierzchniach badawczych wybrano po pięć sosen lub pięć dębów z których pobrano po dwie (z kierunku północnego i wschodniego) dordzeniowe próbki przyrostowe przy użyciu świdra Presslera. Łącznie pozyskano 720 próbek przyrostowych. Próbki zostały zeszlifowane papierami ściernymi o różnych gradacjach, a następnie były skanowane w rozdzielczości 1200 dpi. Do pomiaru szerokości przyrostów rocznych wykorzystano programy CooRecorder i CDendro. Z ostatecznych analiz wykluczono sześć drzew (trzy sosny i trzy dęby) ze względu na niewystarczająco dobrą jakość próbek, które mogłyby wpłynąć negatywnie na wiarygodność wyników. W dalszych analizach uwzględniono przyrosty biomasy nadziemnej z okresu ostatnich pięciu lat (2018-2022).

3.5. Odnowienie naturalne

PUBLIKACJA 2: *Invasive* Prunus serotina *vs.* Robinia pseudoacacia*: How does temperate forest natural regeneration respond to their quantity?*

Inwentaryzację odnowień naturalnych wykonano na 160 powierzchniach badawczych. Na czterech schematycznie rozmieszczonych (na północ, południe, wschód i zachód, w odległości 4,3 m od środka powierzchni) okrągłych poletkach (r = 3 m, 29,3 m^2) policzono odnowienia naturalne wszystkich gatunków z podziałem na tegoroczne (siewki) i młode drzewka do wysokości 130 cm (Kerr i Mackintosh, 2012; Mousavi i in., 2012). Łącznie zinwentaryzowano 24585 osobników reprezentujących 56 gatunków drzew i krzewów.

3.6. Różnorodność biologiczna i skład gatunkowy roślin naczyniowych runa

PUBLIKACJA 3: *Invasive* Prunus serotina *and* Robinia pseudoacacia *impact on understory vegetation is species-, habitat-, and season-specific.*

Spisy florystyczne z użyciem zmodyfikowanej (dziewięciostopniowej) skali Braun-Blanqueta (Barkman i in., 1964) wykonano na 160 powierzchniach badawczych w ramach czterech losowo rozmieszczonych kwadratowych poletkach (25 m^2). W analizach wykorzystano uśrednione pokrycia gatunków dla powierzchni. Łącznie zarejestrowano 205 gatunków roślin naczyniowych. Dane te zostały wykorzystane do obliczenia wskaźników różnorodności biologicznej roślin na trzech poziomach: taksonomicznym, funkcjonalnym (Violle i in., 2007) i filogenetycznym (Tucker i in., 2017). Cechy funkcjonalne roślin potrzebne do obliczenia wskaźników różnorodności funkcjonalnej pozyskano z dostępnych baz danych, takich jak BIEN (Maitner i in., 2018), BioFlor (Klotz i in., 2002), LEDA (Kleyer i in., 2008), czy Pladias (Wild i in., 2019). Uwzględniono cechy funkcjonalne takie jak: specyficzna powierzchnia liścia, maksymalna wysokość, masa nasion, początek i długość kwitnienia, rodzaj zapylenia i ekologiczne liczby wskaźnikowe (Ellenberg i Leuschner, 2010) dla światła, temperatury, wilgotności, żyzności gleby i odczynu gleby.

3.7. Analizy statystyczne

3.7.1. Przyrost biomasy nadziemnej sosen i dębów

PUBLIKACJA 1: *No effect of invasive tree species on aboveground biomass increments of oaks and pines in temperate forests.*

Obliczono względny przyrost biomasy nadziemnej sosen i dębów za ostatnie pięć lat wg wzoru: $relABincr = (AB_{2022} - AB_{2018})/AB_{2022}$

gdzie: *relABincr* – względny przyrost biomasy nadziemnej sosen/dębów, AB_{2022} – biomasa sosen/dębów w 2022 roku, AB_{2018} – biomasa sosen/dębów w 2018 roku. Analizy wykonano na poziomie pojedynczych drzew i drzewostanu.

Na poziomie drzew wykonano uogólnione modele liniowe z efektami stałymi i losowymi (GLMM) z rozkładem beta dla zmiennej objaśnianej tj. względnego przyrostu biomasy nadziemnej sosen/dębów. Jako efekty stałe przyjęto pierśnicę drzew próbnych, udział robinii akacjowej lub czeremchy amerykańskiej w całkowitej biomasie nadziemnej drzewostanu oraz ich interakcje. Jako zmienną losową przyjęto numer identyfikacyjny powierzchni.

Na poziomie drzewostanu zastosowano GLMM z rozkładem beta dla zmiennej objaśnianej tj. względnego przyrostu biomasy nadziemnej sosen/dębów, uwzględniając wiek drzewostanu, udział robinii akacjowej lub czeremchy amerykańskiej w całkowitej biomasie nadziemnej drzewostanu oraz ich interakcje jako zmienne objaśniające. Do wyboru modelu ostatecznego wykorzystano tradycyjne techniki statystyczne bazujące na wartości kryterium informacyjnego Akaikego z zastosowaniem funkcji *dredge()* z pakietu *MuMIn* (Bartoń, 2017), a wyniki przedstawiono za pomocą odpowiedzi brzegowych z wykorzystaniem funkcji *ggpreddict()* z pakietu *ggeffect* (Lüdecke, 2018).

3.7.2. Odnowienie naturalne

PUBLIKACJA 2: *Invasive* Prunus serotina *vs.* Robinia pseudoacacia*: How does temperate forest natural regeneration respond to their quantity?*

Analizy wykonano na danych uśrednionych na poziomie powierzchni badawczej (n=160). Dla składu gatunkowego odnowień naturalnych wykonano kanoniczą analizę korespondencji CCA z użyciem funkcji *cca()* pakietu *vegan* (Oksanen i in., 2018). Uwzględniono wiek drzewostanu i biomasę nadziemną gatunku inwazyjnego jako zmienne modyfikujące rozkład punktów w przestrzeni ordynacyjnej. Wykonano również analizę wartości progowych biomasy gatunków inwazyjnych dla poszczególnych taksonów używając pakietu *TITAN2* (Baker i in., 2023). Wykonano uogólnione modele liniowe z efektami stałymi i losowymi (GLMM) z rozkładami Poissona lub ujemnym dwumianowym (w zależności od poziomu dyspersji modelu określonego przy pomocy testów formalnych) dla zmiennych objaśnianych tj. osobno dla zagęszczenia młodych drzewek i osobno dla jednorocznych siewek. Jako efekty stałe zastosowano wiek drzewostanu i biomasę nadziemną gatunku inwazyjnego drzewa, a jako efekty losowe rok inwentaryzacji odnowienia naturalnego i nadleśnictwo (uwzględniając zależność czasową i przestrzenną między powierzchniami). Wybór modeli finalnych i prezentację wyników wykonano analogicznie do tych opisanych w podrozdziale 3.7.1.

3.7.3. Różnorodność biologiczna i skład gatunkowy roślin naczyniowych runa

PUBLIKACJA 3: *Invasive* Prunus serotina *and* Robinia pseudoacacia *impact on understory vegetation is species-, habitat-, and season-specific.*

Analizy wykonano w oparciu o dane uśrednione na poziomie powierzchni badawczej (n=160). Dla składu gatunkowego roślinności runa wykonano kanoniczą analizę korespondencji CCA (Oksanen i in., 2018). Uwzględniono wiek drzewostanu i biomasę nadziemną gatunku inwazyjnego jako zmienne modyfikujące rozkład punktów w przestrzeni ordynacyjnej. Wykonano również analizę wartości progowych biomasy gatunków inwazyjnych dla poszczególnych taksonów używając pakietu *TITAN2* (Bartoń, 2017). Wykonano uogólnione modele liniowe z efektami stałymi i losowymi (GLMM) z rozkładem normalnym oraz dla bogactwa gatunkowego Poissona lub ujemnym dwumianowym (w zależności od parametrów dyspersji). Modele wykonano dla następujących zmiennych objaśnianych: bogactwa gatunkowego, wskaźnika różnorodności Shannona, bogactwa funkcjonalnego, dyspersji funkcjonalnej, średniej odległości filogenetycznej par gatunków, różnorodności filogenetycznej Faitha oraz średnich ważonych ilościowością (CWM) cech funkcjonalnych (masy nasion, specyficznej powierzchni liścia, maksymalnej wysokości) oraz dla ekologicznych liczb wskaźnikowych (Ellenberg i Leuschner, 2010) dla światła, temperatury, wilgotności, pH gleby i żyzności gleby. W celu obliczenia wskaźników różnorodności filogenetycznej wygenerowano drzewo filogenetyczne dla puli gatunków zidentyfikowanych na powierzchniach badawczych przy użyciu pakietu *VPhylomaker2* (Jin i Qian, 2022), a następnie użyto funkcji *ses.pd()* i *ses.mpd()* z pakietu *picante* (Kambel i in., 2010). Do obliczenia wskaźników różnorodności funkcjonalnej i filogenetycznej zastosowano standaryzowane wielkości efektu (*standardized effect size*; dalej w tekście SES), aby uniknąć wpływu bogactwa gatunkowego na estymację tych zmiennych. Wykorzystano w tym celu model zerowy (losowe permutacje składu gatunkowego dla danej wartości bogactwa gatunkowego) a wartość SES obliczono wg wzoru $SES = (\chi_{obs} - \mu_{perm})/\sigma_{perm}$, gdzie: χ_{obs} – wartość obserwowana, μ_{perm} – średnia z permutacji losowych, σ_{perm} – odchylenie standardowe permutacji, za Czortkiem i in. (2021). W ramach tych obliczeń wykorzystano funcję *dbFD()* z pakietu *FD* (Laliberté i Legendre, 2010) i funkcję *randomizeMatrix()* z pakietu *picante* (Kambel i in., 2010). Dla masy nasion i maksymalnej wysokości zastosowano transformację logarytmiczną (log10). Jako efekty stałe w modelach GLMM

włączono wiek drzewostanu i biomasę nadziemną gatunku inwazyjnego drzewa, a jako efekty losowe rok inwentaryzacji odnowienia naturalnego i nadleśnictwo, aby uwzględnić zależność czasową i przestrzenną. Wybór modeli finalnych i prezentację wyników wykonano analogicznie do tych opisanych w podrozdziale 3.7.1.

4. Wyniki

4.1. Przyrost biomasy nadziemnej sosen i dębów

PUBLIKACJA 1: *No effect of invasive tree species on aboveground biomass increments of oaks and pines in temperate forests.*

Zarówno na poziomie pojedynczych drzew jak i drzewostanu nie wykazano istotnego wpływu udziału biomasy badanych neofitów w całkowitej biomasie drzewostanu na względny przyrost biomasy nadziemnej sosen i dębów. W obu przypadkach obserwowano niewielkie zmniejszenie się względnego przyrostu biomasy nadziemnej sosen i dębów wzdłuż ilościowego gradientu inwazji robinii akacjowej i czeremchy amerykańskiej, jednak wyniki te były nieistotne statystycznie. Udział czeremchy amerykańskiej do 8% i robinii akacjowej do 50% nie powodował znaczących zmian w dynamice przyrostu biomasy drzew rodzimych. Wiek drzewostanu był istotnym predyktorem względnego przyrostu biomasy dla sosen, ale nie dla dębów. Pierśnica natomiast była istotnym predyktorem względnego przyrostu biomasy nadziemnej dla dębów, ale nie dla sosen. Wyniki należy interpretować z pewną ostrożnością ze względu na ograniczoną liczbę powierzchni z bardzo dużym udziałem robinii akacjowej w całkowitej biomasie drzewostanu.

4.2. Odnowienie naturalne

PUBLIKACJA 2: *Invasive* Prunus serotina *vs.* Robinia pseudoacacia*: How does temperate forest natural regeneration respond to their quantity?*

Biomasa nadziemna czeremchy amerykańskiej i robinii akacjowej w sposób istotny kształtowała skład gatunkowy odnowień naturalnych zarówno na siedliskach ubogich

z sosna jak i żyznych z dębem. Analiza CCA wykazała, że na siedliskach ubogich z sosną wraz ze wzrostem biomasy czeremchy amerykańskiej zwiększały się zagęszczenia odnowień *Sorbus aucuparia* i *P. serotina*, a wraz ze wzrostem biomasy robinii akacjowej zwiększały się zagęszczenia odnowień *Sambucus nigra* i *R. pseudoacacia*. Na powierzchniach kontrolnych najczęściej występowały *Betula pendula*, *Pinus sylvestris* i *Quercus petraea*. Na siedliskach żyznych z dębem wraz ze wzrostem biomasy czeremchy amerykańskiej zwiększały się zagęszczenia odnowień *Acer platanoides*, *P. serotina*, *Ulmus minor*, a wraz ze wzrostem biomasy robinii akacjowej zwiększały się zagęszczenia odnowień m.in. *A. platanoides*, *P. serotina*, *S. nigra* i *U. minor*. Z powierzchniami kontrolnymi związane były gatunki takie jak *Q. petraea*, *Carpinus betulus* czy *Crataegus rhipidophylla*.

Analiza TITAN2 wykazała gatunki wskaźnikowe dla zwiększającej się biomasy czeremchy amerykańskiej i robinii akacjowej oraz gatunki które wraz z rosnącą biomasą badanych neofitów zmniejszały swoje zagęszczenia. Z większą biomasą czeremchy amerykańskiej związane były większe zagęszczenia jej odnowienia naturalnego oraz mniejsze dębu bezszypułkowego, zarówno na siedliskach ubogich z sosna jak i na siedliskach żyznych z dębem. Na siedliskach ubogich z sosną z większą biomasą robinii akacjowej związane były wyższe zagęszczenia jej odnowienia naturalnego, *A. platanoides* oraz *S. nigra*, oraz mniejsze *B. pendula*, *P. sylvestris* i *Q. petraea*. Na siedliskach żyznych z dębem obserwowano większe zagęszczenia *A. platanoides*, *R. pseudoacacia* i *Q. robur*, a mniejsze *Q. petraea*.

Analiza modeli GLMM na siedliskach ubogich z sosną wykazała pozytywną zależność biomasy czeremchy amerykańskiej i zagęszczenia młodych drzewek dla czeremchy amerykańskiej i *Sorbus aucuparia*, a negatywną dla sosny zwyczajnej, i obu rodzimych dębów. Na siedliskach żyznych z dębem relacja ta była pozytywna dla czeremchy amerykańskiej, *Prunus padus* i *Fraxinus excelsior*, a negatywna dla *C. betulus* i *Q. petraea*. Na siedliskach ubogich z sosną związek biomasy robinii akacjowej z zagęszczeniem młodych drzewek był pozytywny dla *S. aucuparia* a negatywny dla *Q. petraea* i *R. pseudoacacia*. Na siedliskach żyznych z dębem zależność ta była pozytywna dla 13 gatunków np. wszystkich rodzimych klonów, *Corylus avellana*, *U. minor* i robinii, a negatywna dla *Prunus avium*, *Fagus sylvactica*, *Prunus cerasifera* i *Q. petraea*.

4.3. Różnorodność biologiczna i skład gatunkowy roślin naczyniowych runa

PUBLIKACJA 3: *Invasive Prunus serotina and Robinia pseudoacacia impact on understory vegetation is species-, habitat-, and season-specific.*

Na podstawie analizy CCA wykazano, że biomasa nadziemna neofitów w istotny sposób kształtuje skład gatunkowy roślin naczyniowych runa. Jedynie wiosną na siedlisku żyznym z dębem zasiedlonym przez robinię akacjową wpływ biomasy neofitu nie był istotny statystycznie.

Wiosną nie wykazano gatunków wskaźnikowych dla zwiększającej się biomasy neofitów, poza czeremchą amerykańską na żyznym siedlisku. Według analizy TITAN2 zależność pomiędzy biomasą robinii a pokryciem *Agrostis capillaris* była negatywna, a pokryciem *Corylus avellana* – pozytywna. Latem, na siedliskach ubogich z sosną, związek z biomasą robinii akacjowej był negatywny dla *Melampyrum pratense*, *P. sylvestris*, *Q. petraea* i *Vaccinium myrtillus*, a pozytywny dla dziewięciu gatunków np. *Chelidonium majus*, *Fallopia convolvulus*, *Impatiens parviflora*, czy *Moehringia trinerva*. Na siedliskach żyznych z dębem zależność ta była negatywna dla dębu bezszypułkowego a pozytywna dla dębu szypułkowego, *Ch. majus*, *Dryopteris carthusiana* i *R. pseudoacacia*. Na siedliskach zależność pomiędzy pokryciem gatunku a biomasą czeremchy amerykańskiej była pozytywna dla *D. carthusiana*, *I. parviflora*, *P. serotina* i *Rubus idaeus*. Na siedliskach żyznych z dębem była ona negatywna dla *Oxalis acetosella*, *Pteridium aquilinum* i *Q. petraea*, a pozytywna dla *P. padus* i *P. serotina*.

Biomasa nadziemna robinii akacjowej była pozytywnie skorelowana z bogactwem gatunkowym i wskaźnikiem Shannona na siedliskach lasowych latem. Wiosną na siedliskach borowych wraz ze wzrostem jej biomasy części nadziemnej pozytywnie rosła dyspersja funkcjonalna, a latem różnorodność filogenetyczna, w obu badanych typach siedlisk. Ze średnim filogenetycznym dystansem par gatunków biomasa nadziemna robinii akacjowej była ujemnie skorelowana na siedliskach borowych wiosną, natomiast dodatnio na siedliskach lasowych latem. Biomasa nadziemna czeremchy amerykańskiej była dodatnio skorelowana z bogactwem gatunkowym na siedliskach borowych latem i na siedliskach lasowych wiosną, a także z wartością wskaźnika Shannona na siedliskach lasowych wiosną oraz z bogactwem funkcjonalnym na siedliskach borowych latem. Odnotowano również negatywną zależność biomasy

nadziemnej czeremchy amerykańskiej z dyspersją funkcjonalną na siedliskach lasowych wiosną, natomiast nie stwierdzono istotnych związków z różnorodnością filogenetyczną ani średnim filogenetycznym dystansem par gatunków.

5. Dyskusja

W ramach przedłożonej rozprawy doktorskiej zbadano wpływ inwazyjnych gatunków drzew w gradiencie ich ilości w ekosystemie, wyrażonym biomasą części nadziemnej, na funkcjonowanie i różnorodność biologiczną ekosystemów leśnych. Skupiono się na konsekwencjach dla roślinności runa (Bury i Dyderski, 2025a), odnowienia naturalnego (Bury i Dyderski, 2025b), jak i przyrostu biomasy dojrzałych drzew najwyższego piętra (Bury i Dyderski, 2024). Zbadano nie tylko, czy obecność inwazyjnych drzew wpływa na poszczególne usługi ekosystemowe, ale również zbadano czy, ten wpływ jest zależny od ich ilości (wyrażonej biomasą części nadziemnej), gatunku (robinia akacjowa *vs* czeremcha amerykańska), typu siedliska (ubogie z sosną vs żyzne z dębami) i wieku drzewostanu (potraktowanego jako zmienna ciągła). Uwzględnienie biomasy w badaniach nad inwazją drzew pozwala bardziej szczegółowo zbadać mechanizmy i konsekwencje inwazji. Większa biomasa (Dickie i in., 2011; García i in., 2023; Jagodziński i in. 2024) zwykle jest związana z większymi transformacjami ekosystemu (Richardson i in., 2000) i bardziej widocznym wpływem na poszczególne usługi ekosystemowe. Jak pokazują wyniki uzyskane w mojej pracy doktorskiej, wpływ ten nie jest zerojedynkowy i poszczególne elementy ekosystemu, a nawet gatunki reagują w różny sposób: zarówno pozytywnie jak negatywnie, a dla wielu z nich nie stwierdzono żadnego efektu (Bury i Dyderski, 2024, 2025a,b).

Wykazany brak efektu biomasy czeremchy amerykańskiej i robinii akacjowej na przyrost biomasy nadziemnej sosen i dębów (Bury i Dyderski, 2024) sugeruje równoważenie się dwóch ważnych zjawisk, które zachodzą między drzewami w drzewostanie, a mianowicie o konkurencji i o procesach wspomagania opartych na komplementarności wykorzystania zasobów środowiska (Forrester i Bauhus, 2016; Pretzsch i Forrester, 2017). Można przyjąć, że efekt związany z konkurencją o jedne zasoby (woda, światło) może być równoważony przez zwiększoną podaż innych (większy dopływ substancji odżywczych do gleby). Może też wynikać z ich komplementarności

ze stanem biomasy gatunków rodzimych. Jako że zarówno robinia, jak i czeremcha amerykańska są światłożądne, ich większa biomasa wynika z przerzedzenia koron drzew gatunków rodzimych, które mogły zareagować przyrostem z prześwietlenia. Uzyskane wyniki wskazują, że czeremcha amerykańska i robinia akacjowa w ilościach stwierdzonych na powierzchniach badawczych nie powinny zatem modyfikować zdolności biosekwestracji dwutlenku węgla przez rodzime sosny i dęby.

Wpływ biomasy nadziemnej robinii akacjowej i czeremchy amerykańskiej na odnowienie naturalne (Bury i Dyderski, 2025b) różnicował się ze względu na gatunek inwazyjnego drzewa, gatunek odnowienia i siedlisko. Zależność pomiędzy biomasą czeremchy i robinii akacjowej a zagęszczeniami odnowień naturalnych głównych gatunków lasotwórczych tj. sosny zwyczajnej na siedlisku boru mieszanego świeżego i dębu bezszypułkowego na siedlisku lasu mieszanego świeżego i lasu świeżego była negatywna. Ze zwiększającą się biomasą robinii akacjowej związane było liczniejsze odnowienie naturalne krzewów np. *S. nigra* czy *Euonymus europaeus* oraz gatunków domieszkowych np. rodzimych klonów, *F. excelsior* czy *U. minor*. Zaobserwowano, że w drzewostanach z większą biomasą czeremchy amerykańskiej ten gatunek lepiej się odnawiał. W przypadku robinii akacjowej efekt ten był słabszy. Dodatkowo potwierdzono, że większa biomasa robinii akacjowej wspierała odnawianie się innych gatunków obcego pochodzenia potwierdzając hipotezę „*invasional meltdown*" (Simberloff i Holle, 1999; Riccardi i Simberloff, 2025).

Wpływ biomasy części nadziemnej robinii akacjowej i czeremchy amerykańskiej na skład gatunkowy i różnorodność biologiczną roślin runa różnicował się ze względu na gatunek inwazyjnego drzewa, gatunek rośliny runa, siedlisko i porę roku (Bury i Dyderski, 2025a). Na podstawie uzyskanych wyników można doszukać się pewnych prawidłowości. Geofity jako rośliny które szczyt aktywności mają wiosną nie były wskaźnikami dla rosnącej biomasy nadziemnej badanych neofitów (Rautiainen i in., 2011; Rawlik i in., 2023). Rośliny z tą formą życiową okazują się zatem odporne na postępujące inwazje drzew. Latem gatunków wskaźnikowych było stosunkowo dużo. Wyniki analizy CCA i TITAN2 dla lata były zbieżne. Zaobserwowano, że relacja biomasy inwazyjnych drzew i gatunków ruderalnych, okrajkowych i gatunków leśnych o szerszych skalach ekologicznych była pozytywna. Zależność pomiędzy biomasą neofitów a występowaniem leśnych specjalistów, zwłaszcza na siedliskach ubogich z sosną, była negatywna. Biomasa

części nadziemnej robinii akacjowej i czeremchy amerykańskiej może więc w istotny sposób kształtować różne poziomy różnorodności biologicznej tj. różnorodność taksonomiczną (Wohlgemuth i in., 2022), funkcjonalna i filogenetyczną (Dyderski i Jagodziński, 2021) roślinności runa, jednak kierunek tych zależności jest zróżnicowany w zależności od typu siedliska i pory roku. Pozytywny związek biomasy robinii akacjowej z bogactwem gatunkowym, wskaźnikiem Shannona i różnorodnością filogenetyczną sugeruje, że w pewnych warunkach gatunek ten może sprzyjać wzrostowi złożoności zbiorowisk roślinnych, prawdopodobnie dzięki wzbogaceniu gleby w azot i modyfikacji warunków środowiskowych. Jednocześnie ujemna korelacja ze średnim filogenetycznym dystansem par gatunków w borach wiosną może wskazywać na dominację gatunków o podobnych cechach ekologicznych, co może ograniczać zróżnicowanie sposobów eksploatacji zasobów w krótkim okresie. W przypadku czeremchy amerykańskiej dodatnie zależności z bogactwem gatunkowym, wskaźnikiem Shannona i bogactwem funkcjonalnym mogą wynikać z tworzenia bardziej zróżnicowanych warunków siedliskowych w runie leśnym, np. warunków świetlnych. Z kolei negatywny związek z dyspersją funkcjonalną wiosną na żyznych siedliskach sugeruje, że wysoka biomasa nadziemna czeremchy amerykańskiej może prowadzić do wzrostu podobieństwa cech funkcjonalnych gatunków współwystępujących. Wyniki modeli interpretowane z poparciem analiz CCA i TITAN2, pokazują, że pozytywny wpływ badanych neofitów na wskaźniki różnorodności jest związany ze zwiększającym się pokryciem tylko określonego zestawu gatunków np. *Geranium robertianum* czy *F. convolvulus*, prowadząc do homogenizacji siedlisk (Trentanovi i in., 2013; Šibíková i in., 2019) i utraty specjalistów borowych (Woziwoda i in., 2019; Bury i Dyderski, 2025c). Taka sytuacja może wiązać się ze zmniejszeniem się różnorodności beta (Dyderski i Jagodziński, 2021) i gamma, prowadząc do biotycznej homogenizacji (Olden i in., 2018).

Uzyskane przeze mnie wyniki dotyczące odnowienia naturalnego i roślinności runa zwracają uwagę na konieczność priorytetyzacji działań ochronnych, przede wszystkim siedliskach ubogich z sosną. Zmniejszające się zagęszczenie odnowień naturalnych sosny i zmniejszające się pokrycie specjalistów borowych np. borówki czarnej (Woziwoda i in., 2019; Bury i Dyderski, 2025a) skłania nas do refleksji nad koniecznością lepszej ochrony tych siedlisk. Szczególnie istotne jest to wobec zagrożenia zarówno sosen, jak i borówek zmianami klimatycznymi (Puchałka i in., 2023; Dyderski i in., 2025). Pomimo, że przedstawione badania były przeprowadzone w lasach

gospodarczych, mogą one być również dobrym punktem wyjścia do dyskusji nad lasami, które są chronione w ramach rezerwatów przyrody czy parków narodowych, gdzie występują rzadkie rośliny związane z widnymi drzewostanami sosnowymi na siedliskach ubogich w składniki odżywcze (Bury i in., 2024; Bury i Dyderski, 2025a). Na siedliskach lasowych wpływ badanych neofitów był znacznie mniejszy, co wskazuje na ich większą odporność na inwazje biologiczne światłożądnych gatunków drzew.

W literaturze dostępne są prace poruszające tematykę zarządzania populacjami zarówno robinii akacjowej jak i czeremchy amerykańskiej. Zarówno Sádlo i in. (2017) dla robinii akacjowej, jak i Nyssen, Vanhellemont (2016) oraz Engel i in., (2024) dla czeremchy amerykańskiej podkreślają, że wytyczne postępowania, usuwania bądź integracji, powinny być dostosowane do aktualnych warunków panujących w danym miejscu: składu gatunkowego drzewostanów, typu siedliska, celów hodowlanych oraz kategorii ochronności. Wyniki uzyskane w ramach przedstawionej rozprawy doktorskiej są zgodne z proponowanymi przez cytowanych autorów wytycznymi. Dodatkowo zwracają uwagę na to, że biomasa gatunku inwazyjnego, związana z poziomem inwazji i z reguły czasem jej trwania powinna być traktowana jako prognostyk przyszłych zmian w ekosystemach wywołanych obecnością i dynamiką populacji inwazyjnych drzew.

6. Podsumowanie i wnioski

Reasumując, badanie wpływu inwazyjnych drzew warto przeprowadzać w kontekście ich obfitości. Uwzględnienie biomasy pozwala na realną, bardziej szczegółową ocenę wpływu inwazyjnych drzew na ekosystem leśny. Odrzucono pierwszą hipotezę badawczą, gdyż zarówno w przypadku czeremchy amerykańskiej jak i robinii akacjowej nie wykazano istotnych wyników dla relacji ich biomasy nadziemnej z przyrostami biomasy nadziemnej sosen i dębów. Potwierdzono drugą hipotezę badawczą. Zaobserwowano, że relacja biomas nadziemnych neofitów była negatywnie skorelowana z zagęszczeniami głównych gatunków lasotwórczych, a pozytywnie z zagęszczeniami odnowień drzew domieszkowych i krzewów. Gatunki światłożądne takie jak sosna zwyczajna zmniejszały swoje zagęszczenia a bardziej cienioznośne takie jak wiązy i klony zwiększały swoje zagęszczenia. Potwierdzono również trzecią hipotezę badawczą, gdyż uzyskane wyniki były specyficzne dla gatunku inwazyjnego drzewa jak

i dla gatunków roślinności runa. Dodatkowo potwierdzono, że relacja biomasy nadziemnej neofitu będzie pozytywnie skorelowana z pokryciem gatunków nitrofilnych i leśnych generalistów a negatywnie z pokryciem gatunków acydofilnych i leśnych specjalistów. Zastosowanie różnych metod statystycznych pozwoliło bardziej szczegółowo ocenić realny wpływ gatunków inwazyjnych na roślinność runa. Modele liniowe umożliwiały nam ogólną ocenę ilościową i umożliwiły ocenę, czy dochodzi do wzrostu, czy do spadku różnorodności biologicznej na poszczególnych jej poziomach. Pozostałe analizy umożliwiły nam ocenę jakościową zbiorowisk, pokazując, które gatunki są najbardziej zagrożone a które najbardziej tolerancyjne. Ocena wpływu wzdłuż gradientu ilościowego pozwala na lepsze przewidywanie dalszych skutków inwazji, lepszą ocenę ryzyka i wskazuje na miejsca o najwyższym priorytecie działań gospodarczych i ochronnych. Większa obfitość gatunku inwazyjnego drzewa może, ale nie musi wiązać się ze stratami i problemami dla leśnictwa lub utratą różnorodności biologicznej. Przedstawione badania zwracają uwagę na konieczność priorytetyzacji ochrony siedlisk ubogich z sosną, ze względu na zagrożenie dla odnawiania się na nich głównych gatunków lasotwórczych oraz zagrożenie dla gatunków acydofilnych w runie.

7. Literatura

Aerts, R., Ewald, M., Nicolas, M., Piat, J., Skowronek, S., Lenoir, J., Hattab, T., Garzón-López, C.X., Feilhauer, H., Schmidtlein, S., Rocchini, D., Decocq, G., Somers, B., Van De Kerchove, R., Denef, K., Honnay, O., 2017. Invasion by the Alien Tree *Prunus serotina* Alters Ecosystem Functions in a Temperate Deciduous Forest. Frontiers in Plant Science 8: #179. https://doi.org/10.3389/fpls.2017.00179

Alberti, G., Candido, P., Peressotti, A., Turco, S., Piussi, P., Zerbi, G., 2005. Aboveground biomass relationships for mixed ash (*Fraxinus excelsior* L. and *Ulmus glabra* Hudson) stands in Eastern Prealps of Friuli Venezia Giulia (Italy). Annals of Forest Science 62, 831–836. https://doi.org/10.1051/forest:2005089

Andersen, D., 2019. Secondary human impacts on the forest understory of Ulleung Island, South Korea, a temperate island. Journal of Ecology and Environment 43, #20. https://doi.org/10.1186/s41610-019-0119-2

Baker, M., King, R., Kahle, D., 2023. TITAN2: Threshold Indicator Taxa Analysis. R package version 2.4.3. URL: https://cran.r-project.org/package=TITAN2 (Dostęp: 13.08.2025 r.).

Baraloto, C., Goldberg, D.E., Bonal, D., 2005. Performance Trade-offs among Tropical Tree Seedlings in Contrasting Microhabitats. Ecology 86, 2461–2472. https://doi.org/10.1890/04-1956

Barkman, J.J., Doing, H., Segal, S., 1964. Kritische Bemerkungen und Vorschláge zur quantitativen Vegetationsanalyse. Acta Botanica Neerlandica 13, 394–419. https://doi.org/10.1111/j.1438-8677.1964.tb00164.x

Bärmann, L., Kaufmann, S., Weimann, S., Hauck, M., 2023. Future forests and biodiversity: Effects of Douglas fir introduction into temperate beech forests on plant diversity. Forest Ecology and Management 545, #121286. https://doi.org/10.1016/j.foreco.2023.121286

Bartoń, K., 2017. MuMIn: Multi-Model Inference. URL: https://cran.r-project.org/package=MuMIn (Dostęp: 13.08.2025 r.).

Batavia, C., Nelson, M.P., 2016. Conceptual Ambiguities and Practical Challenges of Ecological Forestry: A Critical Review. Journal of Forestry 114, 572–581. https://doi.org/10.5849/jof.15-103

BDL, 2025. Bank Danych o Lasach. URL: https://www.bdl.lasy.gov.pl/portal/mapy-en (Dostęp: 13.08.2025 r.).

Binkley, D., 1992. Mixtures of N_2-fixing and non-N_2-fixing tree species. W: Cannel, M.G.R., Malcolm, D.C., Robertson, P.A. (red.) The ecology of mixed-species stands of trees. Blackwell Scientific Publications, Oxford. Ss. 92–123.

Bouteiller, X.P., Bussolo, M., Ségura, R., Mariette, S., Porté, A.J., 2023. Considering both sexual and clonal reproduction could help loosen the conflict of use over *Robinia pseudoacacia*. Dendrobiology 90, 30–38. https://doi.org/10.12657/denbio.090.002

Brown, J.K., 1976. Estimating shrub biomass from basal stem diameters. Canadian Journal of Forest Research 6, 153–158. https://doi.org/10.1139/x76-019

Bury, S., Dyderski, M.K., 2025a. Invasive *Prunus serotina* and *Robinia pseudoacacia* impact on understory vegetation is species-, habitat-, and season-specific. NeoBiota 100, 207–238. https://doi.org/10.3897/neobiota.100.151606

Bury, S., Dyderski, M.K., 2025b. Invasive *Prunus serotina* vs. *Robinia pseudoacacia*: How does temperate forest natural regeneration respond to their quantity? NeoBiota 97, 179–213. https://doi.org/10.3897/neobiota.97.135421

Bury, S., Dyderski, M.K., 2025c. Invasive tree species affect terricolous bryophytes biomass and biodiversity in nutrient-poor but not nutrient-rich temperate forests. Scientific Reports 15, #5272. https://doi.org/10.1038/s41598-025-89917-x

Bury, S., Jagodziński, A.M., Dyderski, M.K., 2024. In search of *per capita* effects of *Prunus serotina* Ehrh. invasion on temperate forest understory alpha diversity. Biologia 79, 3011–3025. https://doi.org/10.1007/s11756-024-01766-7

Bury, S., Dyderski, M.K., 2024. No effect of invasive tree species on aboveground biomass increments of oaks and pines in temperate forests. Forest Ecosystems 11, 100201. https://doi.org/10.1016/j.fecs.2024.100201

Castro-Diez, P., Vaz, A.S., Silva, J.S., van Loo, M., Alonso, A., Aponte, C., Bayón, Á., Bellingham, P.J., Chiuffo, M.C., DiManno, N., Kahua, J., Kandert, S., La Porta, N., Marchante, H., Maule, H.G., Mayfield, M.M., Metcalfe, D., Monteverdi, M.C., Nuñez, M.A., Ostertag, R., Parker, I.M., Peltzer, D.A., Potgieter, L.J., Raymundo, M., Rayome, D., Reisman-Berman, O., Richardson, D.M., Roos, R.E., Saldaña, A., Shackleton, R.T., Torres, A., Trudgen, M., Urban, J., Vicente, J.R., Vilà, M., Ylioja, T., Zenni, R.D., Godoy, O., 2019. Global effects of non-native tree species on multiple ecosystem services. Biological Reviews 94, 1477–1501. https://doi.org/10.1111/brv.12511

Chabrerie, O., Loinard, J., Perrin, S., Saguez, R., Decocq, G., 2010. Impact of *Prunus serotina* invasion on understory functional diversity in a European temperate forest. Biological Invasions 12, 1891–1907. https://doi.org/10.1007/s10530-009-9599-9

Chabrerie, O., Verheyen, K., Saguez, R., Decocq, G., 2008. Disentangling relationships between habitat conditions, disturbance history, plant diversity, and American black cherry (*Prunus serotina* Ehrh.) invasion in a European temperate forest: Invasion-disturbance-ecosystem interactions. Diversity and Distributions 14, 204–212. https://doi.org/10.1111/j.1472-4642.2007.00453.x

Cierjacks, A., Kowarik, I., Joshi, J., Hempel, S., Ristow, M., Von Der Lippe, M., Weber, E., 2013. Biological Flora of the British Isles: *Robinia pseudoacacia*. Journal of Ecology 101, 1623–1640. https://doi.org/10.1111/1365-2745.12162

Closset-Kopp, D., Chabrerie, O., Valentin, B., Delachapelle, H., Decocq, G., 2007. When Oskar meets Alice: Does a lack of trade-off in r/K-strategies make *Prunus serotina* a successful invader of European forests? Forest Ecology and Management 247, 120–130. https://doi.org/10.1016/j.foreco.2007.04.023

Corenblit, D., Steiger, J., Tabacchi, E., González, E., Planty-Tabacchi, A.-M., 2014. Ecosystem engineers modulate exotic invasions in riparian plant communities by modifying hydrogeomorphic connectivity: ecosystem engineers modulate exotic invasions. River Research and Applications 30, 45–59. https://doi.org/10.1002/rra.2618

Crooks, J.A., 2002. Characterizing ecosystem-level consequences of biological invasions: the role of ecosystem engineers. Oikos 97, 153–166. https://doi.org/10.1034/j.1600-0706.2002.970201.x

Czortek, P., Adamowski, W., Dyderski, M.K., 2025. Invasive *Prunus cerasifera* alters understory diversity in the early successional oak-hornbeam forests. Biological Invasions 27, #185. https://doi.org/10.1007/s10530-025-03640-2

Czortek, P., Królak, E., Borkowska, L., Bielecka, A., 2023. Effects of surrounding landscape on the performance of *Solidago canadensis* L. and plant functional diversity on heavily invaded post-agricultural wastelands. Biological Invasions 25, 2477–2494. https://doi.org/10.1007/s10530-023-03050-2

Czortek, P., Orczewska, A., Dyderski, M.K., 2021. Niche differentiation, competition or habitat filtering? Mechanisms explaining co-occurrence of plant species on wet meadows of high conservation value. Journal of Vegetation Science 32, e12983. https://doi.org/10.1111/jvs.12983

Deckers, B., Verheyen, K., Vanhellemont, M., Maddens, E., Muys, B., Hermy, M., 2008. Impact of avian frugivores on dispersal and recruitment of the invasive *Prunus serotina* in an agricultural landscape. Biological Invasions 10, 717–727. https://doi.org/10.1007/s10530-007-9164-3

Dickie, I.A., Yates, G.W., John, M.G.St., Stevenson, B.A., Scott, J.T., Rillig, M.C., Peltzer, D.A., Orwin, K.H., Kirschbaum, M.U.F., Hunt, J.E., Burrows, L.E., Barbour, M.M., Aislabie, J., 2011. Ecosystem service and biodiversity trade-offs in two woody successions. Journal of Applied Ecology 48, 926–934. https://doi:10.1111/j.1365-2664.2011.01980.x

Dyderski, M.K., Jagodziński, A.M., 2019a. Similar Impacts of Alien and Native Tree Species on Understory Light Availability in a Temperate Forest. Forests 10, #951. https://doi.org/10.3390/f10110951

Dyderski, M.K., Jagodziński, A.M., 2019b. Seedling survival of *Prunus serotina* Ehrh., *Quercus rubra* L. and *Robinia pseudoacacia* L. in temperate forests of Western Poland. Forest Ecology and Management 450, 117498. https://doi.org/10.1016/j.foreco.2019.117498

Dyderski, M.K., Jagodziński, A.M., 2020. Impacts of alien tree species on the abundance and diversity of terricolous bryophytes. Folia Geobotanica 55, 351–363. https://doi.org/10.1007/s12224-020-09384-2

Dyderski, M.K., Jagodziński, A.M., 2021. Impacts of invasive trees on alpha and beta diversity of temperate forest understories. Biological Invasions 23, 235–252. https://doi.org/10.1007/s10530-020-02367-6

Dyderski, M.K., Paź-Dyderska, S., Jagodziński, A.M., Puchałka, R., 2025. Shifts in native tree species distributions in Europe under climate change. Journal of Environmental Management 373, #123504. https://doi.org/10.1016/j.jenvman.2024.123504

Ellenberg, H., Leuschner, C., 2010. Vegetation Mitteleuropas mit den Alpen in ökologischer, dynamischer und historischer Sicht. UTB, Stuttgart.

Engel, M., Nyssen, B., Desie, E., Den Ouden, J., Raats, L., Hagemann, U., 2024. Managing Black Cherry (*Prunus serotina* Ehrh.) in European Forests: Insights from native and non-native ranges. Forest Ecology and Management 562, #121959. https://doi.org/10.1016/j.foreco.2024.121959

Forrester, D.I., Bauhus, J., 2016. A Review of Processes Behind Diversity—Productivity Relationships in Forests. Current Forestry Reports 2, 45–61. https://doi.org/10.1007/s40725-016-0031-2

Forrester, D.I., Tachauer, I.H.H., Annighoefer, P., Barbeito, I., Pretzsch, H., Ruiz-Peinado, R., Stark, H., Vacchiano, G., Zlatanov, T., Chakraborty, T., Saha, S., Sileshi, G.W., 2017. Generalized biomass and leaf area allometric equations for European tree species incorporating stand structure, tree age and climate. Forest Ecology and Management 396, 160–175. https://doi.org/10.1016/j.foreco.2017.04.011

García, R.A., Fuentes-Lillo, E., Cavieres, L., Cóbar-Carranza, A.J., Davis, K.T., Naour, M., Núñez, M.A., Maxwell, B.D., Lembrechts, J.J., Pauchard, A., 2023. *Pinus contorta*

Alters Microenvironmental Conditions and Reduces Plant Diversity in Patagonian Ecosystems. Diversity 15(3), #320. https://doi.org/10.3390/d15030320

Godefroid, S., Phartyal, S.S., Weyembergh, G., Koedam, N., 2005. Ecological factors controlling the abundance of non-native invasive black cherry (*Prunus serotina*) in deciduous forest understory in Belgium. Forest Ecology and Management 210, 91–105. https://doi.org/10.1016/j.foreco.2005.02.024

Halarewicz, A., 2012. Właściwości ekologiczne i skutki rozprzestrzeniania się czeremchy amerykańskiej *Padus serotina* (Ehrh.) Borkh. w wybranych fitocenozach leśnych. Wydawnictwo Uniwersytetu Przyrodniczego, Wrocław.

Halarewicz, A., Pruchniewicz, D., 2015. Vegetation and environmental changes in a Scots pine forest invaded by *Prunus serotina*: What is the threat to terricolous bryophytes? European Journal of Forest Research 134, 793–801. https://doi.org/10.1007/s10342-015-0890-2

Heberling, J.M., Cassidy, S.T., Fridley, J.D., Kalisz, S., 2019. Carbon gain phenologies of spring-flowering perennials in a deciduous forest indicate a novel niche for a widespread invader. New Phytologist 221, 778–788. https://doi.org/10.1111/nph.15404

Heinrich, G., 1976. Flowering phenologies: bog, woodland, and disturbed habitats. Ecology 57, 890–899. https://doi.org/10.2307/1941055

Horodecki, P., Jagodziński, A.M., 2017. Tree species effects on litter decomposition in pure stands on afforested post-mining sites. Forest Ecology and Management 406, 1–11. https://doi.org/DOI:10.1016/j.foreco.2017.09.059

Jagodziński, A.M., Dyderski, M.K., Gęsikiewicz, K., Horodecki, P., 2019a. Effects of stand features on aboveground biomass and biomass conversion and expansion factors based on a *Pinus sylvestris* L. chronosequence in Western Poland. European Journal of Forest Research 138, 673–683. https://doi.org/10.1007/s10342-019-01197-z

Jagodziński, A.M., Dyderski, M.K., Gęsikiewicz, K., Horodecki, P., 2018. Tree- and Stand-Level Biomass Estimation in a *Larix decidua* Mill. Chronosequence. Forests 9, #587. https://doi.org/10.3390/f9100587

Jagodziński, A.M., Dyderski, M.K., Horodecki, P., Knight, K.S., Rawlik, K., Szmyt, J., 2019b. Light and propagule pressure affect invasion intensity of *Prunus serotina* in a 14-tree species forest common garden experiment. NeoBiota 46, 1–21. https://doi.org/10.3897/neobiota.46.30413

Jagodziński, A.M., Horodecki, P., Jasińska, A.K., Maliński, T., Pilarek, Z., Woźniak, K., Wrońska-Pilarek, D., Zieliński, J., Dyderski, M.K., 2024. Invasive × *Sorbaronia fallax* nothosubsp. *mitschurinii* affects temperate Scots pine forest biodiversity and functioning. Forest Ecology and Management 568, #122147. https://doi.org/10.1016/j.foreco.2024.122147

Jaworski, A., Karczmarek, S., Pach, M., 2007. Hodowla lasu. Tom 2. Sposoby odnowienia lasu. PWRiL, Warszawa.

Jin, Y., Qian, H., 2022. V.PhyloMaker2: An updated and enlarged R package that can generate very large phylogenies for vascular plants. Plant Diversity 44, 335–339. https://doi.org/10.1016/j.pld.2022.05.005

Käber, Y., Bigler, C., HilleRisLambers, J., Hobi, M., Nagel, T.A., Aakala, T., Blaschke, M., Brang, P., Brzeziecki, B., Carrer, M., Cateau, E., Frank, G., Fraver, S., Idoate-Lacasia, J., Holik, J., Kucbel, S., Leyman, A., Meyer, P., Motta, R., Samonil, P., Seebach, L., Stillhard, J., Svoboda, M., Szwagrzyk, J., Vandekerkhove, K., Vostarek, O., Zlatanov, T., Bugmann, H., 2023. Sheltered or suppressed? Tree regeneration in unmanaged European forests. Journal of Ecology 111, 2281–2295. https://doi.org/10.1111/1365-2745.14181

Kambel, S.W., Cowan, P.D., Helmus, M.R., Cornwell, W.K., Morlon, H., Ackerly, S.P., Blomberg, S.P., Webb, C.O., 2010. Picante: R tools for integrating phylogenies and ecology. Bioinformatics 26:1463-1464.

Kanzler, M., Böhm, C., Freese, D., 2021. The development of soil organic carbon under young black locust (*Robinia pseudoacacia* L.) trees at a post-mining landscape in eastern Germany. New Forests 52, 47–68. https://doi.org/10.1007/s11056-020-09779-1

Kerr, G., Mackintosh, H., 2012. Long-Term Survival of Saplings during the Transformation to Continuous Cover. Forests 3, 787–798. https://doi.org/10.3390/f3030787

Kleyer, M., Bekker, R.M., Knevel, I.C., Bakker, J.P., Thompson, K., Sonnenschein, M., Poschlod, P., van Groenendael, J.M., Klimeš, L., Klimešová, J., Klotz, S., Rusch, G.M., Hermy, M., Adriaens, D., Boedeltje, G., Bossuyt, B., Dannemann, A., Endels, P., Götzenberger, L., Hodgson, J.G., Jackel, A.-K., Kühn, I., Kunzmann, D., Ozinga, W.A., Römermann, C., Stadler, M., Schlegelmilch, J., Steendam, H.J., Tackenberg, O., Wilmann, B., Cornelissen, J.H.C., Eriksson, O., Garnier, E., Peco, B., 2008. The LEDA

Traitbase: a database of life-history traits of the Northwest European flora. Journal of Ecology 96, 1266–1274. https://doi.org/10.1111/j.1365-2745.2008.01430.x

Klotz, S., Kühn, I., Durka, W., 2002. BIOLFLOR – Eine Datenbank zu biologisch-ökologischen Merkmalen der Gefäßpflanzen in Deutschland. Schriftenreihe für Vegetationskunde. Bundesamt für Naturschutz, Bonn.

Komisja Europejska (red.), 2023. Guidelines on closer-to-nature forest management. EU Publications Office, Luxembourg. https://doi.org/10.2779/898789

Kudo, G., Ida, T.Y., Tani, T., 2008. Linkages between phenology, pollination, photosynthesis, and reproduction in deciduous forest understory plants. Ecology 89, 321–331. https://doi.org/10.1890/06-2131.1

Kurek, P., Wiatrowska, B., Piechnik, Ł., Holeksa, J., 2024. Phenological gap in fruiting period and dispersal of seeds from alien fleshy-fruited plants by medium-sized carnivores in temperate forests of Central Europe. NeoBiota 93, 321–337. https://doi.org/10.3897/neobiota.93.128008

Kutnar, L., Nagel, T.A., Kermavnar, J., 2019. Effects of Disturbance on Understory Vegetation across Slovenian Forest Ecosystems. Forests 10, #1048. https://doi.org/10.3390/f10111048

Laliberté, E., Legendre, P., 2010. A distance-based framework for measuring functional diversity from multiple traits. Ecology 91, 299–305. https://doi.org/10.1890/08-2244.1

Lazzaro, L., Mazza, G., d'Errico, G., Fabiani, A., Giuliani, C., Inghilesi, A.F., Lagomarsino, A., Landi, S., Lastrucci, L., Pastorelli, R., Roversi, P.F., Torrini, G., Tricarico, E., Foggi, B., 2018. How ecosystems change following invasion by *Robinia pseudoacacia*: Insights from soil chemical properties and soil microbial, nematode, microarthropod and plant communities. Science of The Total Environment 622–623, 1509–1518. https://doi.org/10.1016/j.scitotenv.2017.10.017

Lüdecke, D., 2018. ggeffects: Tidy Data Frames of Marginal Effects from Regression Models. Journal of Statistical Software 3, #772. https://doi.org/10.21105/joss.00772

Maitner, B.S., Boyle, B., Casler, N., Condit, R., Donoghue, J., Durán, S.M., Guaderrama, D., Hinchliff, C.E., Jørgensen, P.M., Kraft, N.J.B., McGill, B., Merow, C., Morueta-Holme, N., Peet, R.K., Sandel, B., Schildhauer, M., Smith, S.A., Svenning, J., Thiers, B., Violle, C., Wiser, S., Enquist, B.J., 2018. The BIEN R package: A tool to access the Botanical

Information and Ecology Network (BIEN) database. Methods in Ecology and Evolution 9, 373–379. https://doi.org/10.1111/2041-210X.12861

Matuszkiewicz, W., 2001. Przewodnik do oznaczania zbiorowisk roślinnych Polski. Wydawnictwo Naukowe PWN, Warszawa.

Milanović, M., Knapp, S., Pyšek, P., Kühn, I., 2020. Linking traits of invasive plants with ecosystem services and disservices. Ecosystem Services 42, #101072. https://doi.org/10.1016/j.ecoser.2020.101072

Mousavi, K.S.A., Ali Roshani, G., Jalali, S.G., Shahrdami, A., 2012. The Effects of Cover Crown, Percentage and Slope Aspect on the Quantitative Distribution of the Alder's Saplings in Forests of North of Iran. Resources and Environment 2, 17–20. https://doi.org/10.5923/j.re.20120201.02

Muys, B., Maddelein, D., Lust, N., 1992. Ecology, practice and policy of black cherry (*Prunus serotina* Ehrh.) management in Belgium. Silva Gandavensis 57, 28–45. https://doi.org/10.21825/sg.v57i0.885

Namura-Ochalska, A., Borowa, B., 2015. Walka z czeremchą amerykańską *Padus serotina* (Ehrh.) Borkh. w leśnictwie Rózin w Kampinoskim Parku Narodowym; ocena skuteczności wybranych metod. W: Krzysztofiak, L., Krzysztofiak, A. (red.), Inwazyjne gatunki obcego pochodzenia zagrożeniem dla rodzimej przyrody. Stowarzyszenie "Człowiek i Przyroda," Krzywe. Ss. 127–142.

Nicolescu, V.-N., Rédei, K., Mason, W.L., Vor, T., Pöetzelsberger, E., Bastien, J.-C., Brus, R., Benčať, T., Đodan, M., Cvjetkovic, B., Andrašev, S., La Porta, N., Lavnyy, V., Mandžukovski, D., Petkova, K., Roženbergar, D., Wąsik, R., Mohren, G.M.J., Monteverdi, M.C., Musch, B., Klisz, M., Perić, S., Keça, L., Bartlett, D., Hernea, C., Pástor, M., 2020. Ecology, growth and management of black locust (*Robinia pseudoacacia* L.), a non-native species integrated into European forests. Journal of Forestry Research 31, 1081–1101. https://doi.org/10.1007/s11676-020-01116-8

Nyssen, B., Ouden, J.D., Bindewald, A., Brancalion, P., Kremer, K., Lapin, K., Raats, L., Schatzdorfer, E., Stanturf, J., Verheyen, K., Muys, B., 2024. Established Invasive Tree Species Offer Opportunities for Forest Resilience to Climate Change. Current Forestry Reports 10, 456–486. https://doi.org/10.1007/s40725-024-00232-6

Nyssen, B., Vanhellemont, M., 2016. 5.6 Integrating black cherry in forest management in the Netherlands and Belgium. W: Krumm F, Vítková L (red.) Introduced tree

species in European forests: opportunities and challenges. European Forest Institute, Joensuu. Ss. 362–372.

Oksanen, J., Blanchet, F., Kindt, R., 2018. "vegan" 2.3.3. - Community Ecology Package. URL: https://cran.r-project.org/package=vegan (Dostęp: 13.08.2025 r.).

Olden, J.D., Comte, L., Giam, X., 2018. The Homogocene: a research prospectus for the study of biotic homogenisation. NeoBiota 37, 23–36. https://doi.org/10.3897/neobiota.37.22552

Oliver, C.D., Larson, B.A., 1996. Forest Stand Dynamics, Update Edition. Yale School of the Environment Other Publications. John Wiley & Sons, New York.

Oluwajuwon, T.V., Chazdon, R.L., Ota, L., Gregorio, N., Herbohn, J., 2024. Bibliometric and literature synthesis on assisted natural regeneration: an evidence base for forest and landscape restoration in the tropics. Frontiers in Forests and Global Change 7, #1412075. https://doi.org/10.3389/ffgc.2024.1412075

Palik, B.J., D'Amato, A.W., 2017. Ecological Forestry: Much More Than Retention Harvesting. Journal of Forestry 115, 51–53. https://doi.org/10.5849/jof.16-057

Parker, I.M., Simberloff, D., Lonsdale, W.M., Goodell, K., Wonham, M., Kareiva, P.M., Williamson, M.H., Von Holle, B., Moyle, P.B., Byers, J.E., Goldwasser, L., 1999. Impact: toward a framework for understanding the ecological effects of invaders. Biological Invasions 1, 3–19. https://doi.org/10.1023/A:1010034312781

Pearse, I.S., Sofaer, H.R., Zaya, D.N., Spyreas, G., 2019. Non-native plants have greater impacts because of differing per-capita effects and nonlinear abundance–impact curves. Ecology Letters 22, 1214–1220. https://doi.org/10.1111/ele.13284

Petri, L., Ibáñez, I., 2024. Trait-related functional changes in understory forest community after invasion are driven by complementarity rather than displacement. Frontiers in Ecology and Evolution 12, #1325275. https://doi.org/10.3389/fevo.2024.1325275

Pretzsch, H., Forrester, D.I., 2017. Stand dynamics of mixed-species stands compared with monocultures. W: Pretzsch, H., Forrester, D., Bauhus, J. (red.) Mixed-Species Forests: Ecology and Management. Springer, Berlin. Ss. 117–209.

Puchałka, R., Paź-Dyderska, S., Woziwoda, B., Dyderski, M.K., 2023. Climate change will cause climatic niche contraction of *Vaccinium myrtillus* L. and *V. vitis-idaea* L. in Europe. Science of The Total Environment 892, #164483. https://doi.org/10.1016/j.scitotenv.2023.164483

Rautiainen, M., Mõttus, M., Heiskanen, J., Akujärvi, A., Majasalmi, T., Stenberg, P., 2011. Seasonal reflectance dynamics of common understory types in a northern European boreal forest. Remote Sensing of Environment 115, 3020–3028. https://doi.org/10.1016/j.rse.2011.06.005

Rawlik, K., Rawlik, M., Jagodziński, A.M., 2023. Seasonal dynamics of herbaceous layer biomass and its contribution to annual net primary production in an oak–hornbeam forest. Forest Ecology and Management 544, #121195. https://doi.org/10.1016/j.foreco.2023.121195

Ricciardi, A., Simberloff, D., 2025. Revisiting invasional meltdown: mechanisms and consequences of positive non-native species interactions. Biological Invasions 27, #183. https://doi.org/10.1007/s10530-025-03625-1

Rice, S.K., Westerman, B., Federici, R., 2004. Impacts of the Exotic, Nitrogen-Fixing Black Locust (*Robinia pseudoacacia*) on Nitrogen- Cycling in a Pine-Oak Ecosystem. Plant Ecology 174, 97–107. https://doi.org/10.1023/B:VEGE.0000046049.21900.5a

Richardson, D.M., Pysek, P., Rejmanek, M., Barbour, M.G., Panetta, F.D., West, C.J., 2000. Naturalization and invasion of alien plants: concepts and definitions. Diversity and Distributions 6, 93–107. https://doi.org/10.1046/j.1472-4642.2000.00083.x

Sádlo, J., Vítková, M., Pergl, J., Pyšek, P., 2017. Towards site-specific management of invasive alien trees based on the assessment of their impacts: the case of *Robinia pseudoacacia*. NeoBiota 35, 1–34. https://doi.org/10.3897/neobiota.35.11909

Šibíková, M., Jarolímek, I., Hegedüšová, K., Májeková, J., Mikulová, K., Slabejová, D., Škodová, I., Zaliberová, M., Medvecká, J., 2019. Effect of planting alien *Robinia pseudoacacia* trees on homogenization of Central European forest vegetation. Science of The Total Environment 687, 1164–1175. https://doi.org/10.1016/j.scitotenv.2019.06.043

Simberloff, D., Holle, B.V., 1999. Positive Interactions of Nonindigenous Species: Invasional Meltdown? Biological Invasions 1, 21–32. http://dx.doi.org/10.1023/A:1010086329619

Slabejová, D., Čejka, T., Hegedüšová, K., Májeková, J., Medvecká, J., Mikulová, K., Šibíková, M., Škodová, I., Šustek, Z., Jarolímek, I., 2023. Comparison of alien *Robinia pseudoacacia* stands with native forest stands across different taxonomic groups. Forest Ecology and Management 548, #121413. https://doi.org/10.1016/j.foreco.2023.121413

Stanek, M., Piechnik, Ł., Stefanowicz, A.M., 2020. Invasive red oak (*Quercus rubra* L.) modifies soil physicochemical properties and forest understory vegetation. Forest Ecology and Management 472, #118253. https://doi.org/10.1016/j.foreco.2020.118253

Starfinger, U., Kowarik, I., Rode, M., Schepker, H., 2003. From Desirable Ornamental Plant to Pest to Accepted Addition to the Flora? – the Perception of an Alien Tree Species Through the Centuries. Biological Invasions 5, 323–335. https://doi.org/10.1023/B:BINV.0000005573.14800.07

Trentanovi, G., Ziechmann, U., Kowarik, I., Cierjacks, A., 2013. Biotic homogenization at the community scale: disentangling the roles of urbanization and plant invasion. Diversity and Distributions 19, 738–748. https://doi.org/10.1111/ddi.12028

Tucker, C.M., Cadotte, M.W., Carvalho, S.B., Davies, T.J., Ferrier, S., Fritz, S.A., Grenyer, R., Helmus, M.R., Jin, L.S., Mooers, A.O., Pavoine, S., Purschke, O., Redding, D.W., Rosauer, D.F., Winter, M., Mazel, F., 2017. A guide to phylogenetic metrics for conservation, community ecology and macroecology: A guide to phylogenetic metrics for ecology. Biological Reviews 92, 698–715. https://doi.org/10.1111/brv.12252

Vilà, M., Trillo, A., Castro-Díez, P., Gallardo, B., Bacher, S., 2024. Field studies of the ecological impacts of invasive plants in Europe. NeoBiota 90, 139–159. https://doi.org/10.3897/neobiota.90.112368

Violle, C., Navias, M.-L., Vile, D., Kazakou, E., Fortunel, C., Hummel, I., Garnier, E., 2007. Let the concept of trait be functional! Oikos 116, 882–892. https://doi.org/10.1111/j.0030-1299.2007.15559.x

Vítková, M., Müllerová, J., Sádlo, J., Pergl, J., Pyšek, P., 2017. Black locust (*Robinia pseudoacacia*) beloved and despised: A story of an invasive tree in Central Europe. Forest Ecology and Management 384, 287–302. https://doi.org/10.1016/j.foreco.2016.10.057

Wiatrowska, B., Kurek, P., Moroń, D., Celary, W., Chrzanowski, A., Trzciński, P., Piechnik, Ł., 2023. Linear scaling – negative effects of invasive *Spiraea tomentosa* (Rosaceae) on wetland plants and pollinator communities. NeoBiota 81, 63–90. https://doi.org/10.3897/neobiota.81.95849

Wild, J., Kaplan, Z., Danihelka, J., Petřík, P., Chytrý, M., Novotný, P., Rohn, M., Šulc, V., Brůna, J., Chobot, K., Ekrt, L., Holubová, D., Knollová, I., Kocián, P., Štech, M., Štěpánek, J.,

Zouhar, V., 2019. Plant distribution data for the Czech Republic integrated in the Pladias database. Preslia 91, 1–24. https://doi.org/10.23855/preslia.2019.001

Wohlgemuth, T., Gossner, M.M., Campagnaro, T., Marchante, H., van Loo, M., Vacchiano, G., Castro-Díez, P., Dobrowolska, D., Gazda, A., Keren, S., Keserű, Z., Koprowski, M., La Porta, N., Marozas, V., Nygaard, P.H., Podrázský, V., Puchałka, R., Reisman-Berman, O., Straigytė, L., Ylioja, T., Pötzelsberger, E., Silva, J.S., 2022. Impact of non-native tree species in Europe on soil properties and biodiversity: a review. NeoBiota 78, 45–69. https://doi.org/10.3897/neobiota.78.87022

Woziwoda, B., Dyderski, M.K., Jagodziński, A.M., 2019. Effects of land use change and *Quercus rubra* introduction on *Vaccinium myrtillus* performance in *Pinus sylvestris* forests. Forest Ecology and Management 440, 1–11. https://doi.org/10.1016/j.foreco.2019.03.010

Younginger, B.S., Sirová, D., Cruzan, M.B., Ballhorn, D.J., 2017. Is biomass a reliable estimate of plant fitness? Applications in Plant Sciences 5, #1600094. https://doi.org/10.3732/apps.1600094

Zasada, M., 2017. Raport końcowy z tematu badawczego "Ekologiczne, gospodarcze i urządzeniowe konsekwencje występowania wybranych gatunków drzew obcych w Polsce" realizowanego w latach 2013-2017 przez Samodzielną Pracownię Dendrometrii i Nauki o Produkcyjności Lasu na zlecenie Dyrekcji Generalnej Lasów Państwowych w Warszawie. SGGW, Warszawa.

Oświadczenia

Oświadczenie kierującego pracą

Oświadczam, że niniejsza praca została przygotowana pod moim kierunkiem i stwierdzam, że spełnia ona warunki do przedstawienia jej w postępowaniu o nadanie stopnia doktora nauk biologicznych.

Kórnik, 14.08.2025 r.

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podpis

Oświadczenie autora pracy

Świadomy odpowiedzialności prawnej oświadczam, że niniejsza rozprawa doktorska została napisana przeze mnie samodzielnie i nie zawiera treści uzyskanych w sposób niezgodny z obowiązującymi przepisami.

Oświadczam również, że przedstawiona praca nie była wcześniej przedmiotem procedur związanych z uzyskaniem stopnia doktora w innej jednostce.

Oświadczam ponadto, że niniejsza wersja pracy jest identyczna z załączoną wersją elektroniczną.

Sebastian Bury

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Kórnik, 14.08.2025 r. podpis

mgr inż. Sebastian Piotr Bury

Instytut Dendrologii Polskiej Akademii Nauk

Zakład Ekologii

Kórnik, 14.08.2025 r.

OŚWIADCZENIE

Oświadczam, że w pracy:

Bury S., Dyderski M.K. 2024. No effect of invasive tree species on aboveground biomass increments of oaks and pines in temperate forests. Forest Ecosystems 11: 100201. https://doi.org/10.1016/j.fecs.2024.100201

Mój wkład w powstanie tej pracy polegał na udziale w opracowaniu koncepcji i metodyki badań, przeglądzie literatury związanej z analizowanym zagadnieniem, zbiorze danych w terenie, opracowaniu wyników i ich analizie statystycznej oraz na przygotowaniu manuskryptu pracy i wykonaniu korekty manuskryptu artykułu wg uzyskanych recenzji; pełniłem również rolę autora korespondencyjnego. **Mój udział procentowy szacuję na 80%.**

Bury S., Dyderski M.K. 2025. Invasive *Prunus serotina* vs. *Robinia pseudoacacia*: How does temperate forest natural regeneration respond to their quantity? NeoBiota 97: 179–213. https://doi.org/10.3897/neobiota.97.135421

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M. Dyd

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Podpis

Załączniki

Publikacja 1.

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No effect of invasive tree species on aboveground biomass increments of oaks and pines in temperate forests

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ABSTRACT

Prunus serotina and *Robinia pseudoacacia* are the most widespread invasive trees in Central Europe. In addition, according to climate models, decreased growth of many economically and ecologically important native trees will likely be observed in the future. We aimed to assess the impact of these two neophytes, which differ in the biomass range and nitrogen-fixing abilities observed in Central European conditions, on the relative aboveground biomass increments of native oaks *Quercus robur* and *Q. petraea* and Scots pine *Pinus sylvestris*. We aimed to increase our understanding of the relationship between facilitation and competition between woody alien species and overstory native trees. We established 72 circular plots (0.05 ha) in two different forest habitat types and stands varying in age in western Poland. We chose plots with different abundances of the studied neophytes to determine how effects scaled along the quantitative invasion gradient. Furthermore, we collected growth cores of the studied native species, and we calculated aboveground biomass increments at the tree and stand levels. Then, we used generalized linear mixed-effects models to assess the impact of invasive species abundances on relative aboveground biomass increments of native tree species. We did not find a biologically or statistically significant impact of invasive *R. pseudoacacia* or *P. serotina* on the relative aboveground biomass increments of native oaks and pines along the quantitative gradient of invader biomass or on the proportion of total stand biomass accounted for by invaders. The neophytes did not act as native tree growth stimulators but also did not compete with them for resources, which would escalate the negative impact of climate change on pines and oaks. The neophytes should not significantly modify the carbon sequestration capacity of the native species. Our work combines elements of the *per capita* effect of invasion with research on mixed forest management.

1. Introduction

The ecology and biology of invasive species have been studied for decades, but, due to their increasing threat to nature and the human economy, they are still important scientific topics (Heger et al., 2021; Kotta, 2023; Roy et al., 2023). Although they have been intensively studied, we still do not know enough about the full roles of invasive trees or their consequences for native ecosystems (Roy et al., 2023). In many places, invasive trees have become a permanent part of the indigenous landscape. Furthermore, many of them, apart from negative consequences such as loss of biodiversity (e.g., García et al., 2023; Wohlgemuth et al., 2022; Woziwoda et al., 2021), also provide positive ecosystem services, including provisional services like supplying timber products and natural medicines, increasing the total productivity of ecosystems, regulating services (e.g., erosion control), and supporting services (e.g., providing habitats for wildlife or cultural services; Castro-Diez et al., 2019). In many respects, the ambiguous status of invasive tree species is additionally complicated by difficulties in their management, in particular their costly, labor-intensive, and often unsuccessful eradication from the natural environment (Namura-Ochalska and Borowa, 2015; Nyssen and Vanhellemont, 2016; Vítková et al., 2017). For these reasons, some researchers discouraged by the unsuccessful fight are changing their attitude towards invasive trees, not treating them as clear enemies but trying to integrate them into local ecosystems, as with *Prunus serotina* Ehrh., for example in the Netherlands (Nyssen and Vanhellemont, 2016).

Mixed forests account for 17% of the total forest area in Europe (Korhonen et al., 2020). Mixed-species stands are usually more resistant to various natural disturbances, such as insect outbreaks, floods, wind damage, and long-term droughts (Bauhus et al., 2017a; Jactel et al., 2009). This resilience is primarily associated with the diversification of silviculture risk over time and space (Pretzsch, 2009; Szymański, 2001).

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Mixed forests may decrease the economic value of stands, but they offer an important benefit for administrators who are careful about risks. For decision-makers concerned with balancing economic gains in forestry amidst uncertainties like market changes and natural disasters, mixed forests provide a significant reduction in these risks (Knoke et al., 2005). However, it should be emphasized that, over time, more studies have confirmed the advantage of mixed stands over monocultures in terms of productivity (Liang et al., 2016; Ruiz-Benito et al., 2014; Thurm and Pretzsch, 2016). Mixed-species forests also provide a greater variety of natural habitats, thereby significantly increasing biodiversity (Röhle, 2018). Additionally, in comparison to monoculture, they have a different impact on the quality of the forest litter and decomposition (Horodecki et al., 2019) and on soil chemical and microbial properties (Yang et al., 2022), and they are considered to be more efficient at climate change mitigation (Warner et al., 2023). Individual species vary in their susceptibility to different stresses and exhibit different mortality rates, growth dynamics, and growth regeneration after exposure to stress. This means that, at the forest stand level or broadly in the forest complexes, there is a higher chance of the survival of at least a portion of the forest (Jactel et al., 2009).

In the past, in Central Europe, foresters were interested in planting exotic trees. They introduced numerous tree species from North America as admixtures, for example, *Pseudotsuga menziesii* (Mirb.) Franco (Ronch et al., 2016), *Quercus rubra* L. (Dyderski et al., 2020), *Robinia pseudoacacia* L. (Cierjacks et al., 2013; Slabejová et al., 2023), and *P. serotina* (Aerts et al., 2017; Starfinger et al., 2003). They believed that all of those species could provide many ecosystem services, like timber production (Aerts et al., 2017; Ronch et al., 2016) and soil improvement (Starfinger et al., 2003). For example, according to studies in Germany, *P. menziesii* can form very productive stands with *Fagus sylvatica* (Thurm and Pretzsch, 2016). Some of these species, like *P. menziesii*, had good applications to forestry in Central Europe, but others did not and also turned out to be invasive, like *P. serotina* (Starfinger et al., 2003). Setting aside the controversies surrounding invasive tree species, the similarly interesting processes of facilitation and competition with native species can be observed and should be studied.

Invasive tree species are often referred as "transformers", that is, species able to transform habitat conditions, as they can significantly alter ecosystems they have newly colonized (Aerts et al., 2017; Richardson et al., 2000). These transformations can have varied effects on individual ecosystem services, both positive and negative (Castro-Diez et al., 2019). They can negatively impact acidophilous vegetation (Woziwoda et al., 2021) but may promote nitrophilous plants (Slabejová et al., 2023). Not every habitat is equally susceptible to invasive species entry and further development of an invasion. The impacts on different ecosystem services can also vary. This demonstrates the context-dependence of biological invasions (Sapsford et al., 2020). It is often stated that coniferous forests on nutrient-poor soils are more susceptible to invasions and the negative effects of invasive species transformations than are deciduous forests on nutrient-rich soils (Chmura, 2004; Halarewicz, 2011). Considering global climatic changes, studies on the assimilation of invasive species, which may benefit from these changes while having a negative impact on native species, are important (Dukes and Mooney, 1999; Dyderski et al., 2018; Puchałka et al., 2023).

The radial growth of trees, which is crucial for biomass increments, depends on various factors (Rumyantseva et al., 2023). Apart from species-specific growth trends, environmental factors such as climate, soil, and competition play a significant role in shaping trees' increments (Kahveci and Arslan, 2021). Soil and light conditions influence tree growth, and modifications of these conditions are also observed when invasive trees enter an ecosystem (Aerts et al., 2017; Richardson et al., 2000). For this study, we were interested in whether the described competition and facilitation phenomena (Forrester and Bauhus, 2016), which are based on the principles of resource complementarity (Pretzsch and Forrester, 2017), are directly observable in changes in tree growth and, consequently, in the overall aboveground biomass increment. This complementarity can be modified by various factors like topography or soil pH (Mina et al., 2018). Species abundance can be related to either their presence in the overstory or the formation of a dense subcanopy or shrub layer. There are studies revealing the impacts on overstory tree growth in both the understory (Giuggiola et al., 2018) and species mixtures in the overstory (Vannoppen et al., 2019). In bilateral relations between two species, competition may be reduced when interspecific competition is lower than intraspecific competition, or facilitation may occur when one species favorably affects the other (Ammer, 2019; Rebola-Lichtenberg et al., 2021). In the context of different uses of environmental resources, it is also worth mentioning the variability of functional traits such as wood density, specific leaf area, different depths of root systems, and the ability to fix nitrogen (Bauhus et al., 2017b). Particular tree species representing specific functional types have different impacts on other trees and occupy different niches.

Our study explored competition and facilitation in a mixed forest. There are few papers discussing the *per capita* effects of plant invasion, and they usually focus on invaded versus non-invaded sites. So far, such papers have explored the functional diversity of plants (Czortek et al., 2023), species richness of plants and pollinating insects (Wiatrowska et al., 2023), native and non-native plant species richness and abundance, and soil characteristics, microclimate, and light interception (García et al., 2023). However, to date, quantitative assessments of the *per capita* effects of invasive tree species on native tree growth have been not published. Such an approach could be helpful in investigating how the effects of invasive species change during different phases of invasion, which are characterized by the abundance of the studied species.

We aimed to assess the impact of two invasive tree species, black cherry *P. serotina* and black locust *R. pseudoacacia*, on aboveground biomass increments of Scots pine *Pinus sylvestris* L. and the oaks *Q. robur* L. and *Q. petraea* (Matt.) Liebl. in temperate forests. We hypothesized that (H1) both neophytes would impact the aforementioned ecosystem services based on the unknown overlap between competition and facilitation processes occurring between different tree species. We expected (H2) differences between *P. serotina* and *R. pseudoacacia* in the magnitude of their effects due to differences in biology and ecology, as both differ in nitrogen uptake strategy. Moreover, the biomass, abundance, and size of these two neophytes differ in Central Europe. As *R. pseudoacacia* reaches larger sizes than *P. serotina*, the *R. pseudoacacia* biomass gradient is wider. Finally, (H3) we hypothesized that the impacts would vary along the quantitative invasion gradient, as described by the general phenomenon of the *per capita* effect of an invasion (Parker et al., 1999; Pearse et al., 2019; Sapsford et al., 2020). Young and adult individuals differently impact soil, water, and light conditions. Our study should be important for invasive tree species management, especially in the context of the expected climate change mitigation potential of forests, which are one of the most important carbon sinks (Pan et al., 2011; Turner et al., 1995). Tree species differ in their capacity for carbon sequestration, which is also dependent on tree age. Therefore, additional stand species-mixing and stand structure studies should be conducted. Our study is an important contribution that will allow us to better manage invasive species. It broadens the perspective on this issue and should make decision-making easier. Different plant species are managed slightly differently due to their different biology and ecology. Additionally, their abundance, size, and layer of occurrence are important. Each case must be considered individually because there are different costs and benefits associated with removing a particular tree or leaving it in the ecosystem.

2. Materials and methods

2.1. Invasive species studied

2.1.1. Robinia pseudoacacia

Robinia pseudoacacia, commonly called black locust, naturally occurs in North America. *R. pseudoacacia* seeds are spread mostly by wind, but

also by water, by falling beneath the canopy of parental trees (Morimoto et al., 2010), and by animals (Cierjacks et al., 2013; Gams, 1924). This species also reproduces vegetatively through root suckers (Bouteiller et al., 2023). *Robinia pseudoacacia* is a light-demanding species and grows well on soils of various fertility and pH, but it does not tolerate wet or strongly compacted soils (Cierjacks et al., 2013; Huntley, 1990). *Robinia pseudoacacia* stands, because of their loose canopies, are usually very bright, which affects understory microclimatic conditions, especially air humidity and temperature (Slabejová et al., 2023). One of the most important elements of the biology and ecology of this species is its symbiosis with nitrifying bacteria and the consequent enrichment of nitrogen in the soil (Binkley, 1992; Kanzler et al., 2021; Slabejová et al., 2023).

2.1.2. *Prunus serotina*

Prunus serotina, commonly called black cherry, naturally occurs in the eastern part of North America. In Central Europe, *P. serotina* is usually a shrub and less frequently a low tree, and it grows in different types of habitats, from dry and nutrient-poor to wet and fertile (Otręba, 2016; Starfinger et al., 2003). The use of and attitudes towards *P. serotina* have varied since the time of its introduction. Initially, it was planted as an ornamental tree. In the past, it was hoped that it would be a timber-productive species even on poor soils, as well as a soil improver or a wind and fire break. The reality turned out to be slightly different, and over time *P. serotina* began to be controlled and treated as forest pest due to its invasive nature and poor productivity. Then, black cherries started to become more acceptable (Starfinger et al., 2003). Nowadays, *P. serotina* has assimilated into local forests in Western Europe, for example, in the Netherlands and Belgium (Nyssen and Vanhellemont, 2016). In Poland, *P. serotina* is considered a forest weed that impedes the artificial and natural regeneration of stands, especially those of pine trees. At the moment, the assimilation of *P. serotina* is not promoted, and the species will not be introduced to forests.

2.2. Study area

We conducted this study in two different forest types typical of Central Europe. The first was the *Leucobryo-Pinetum* W. Mat. (1962) 1973 community, which is dominated by *P. sylvestris* and grows on nutrient-poor soils, such as podzols, cambic arenosols, and arenosols, as well as in secondary pine forest with visible anthropogenic disturbances. The other forest type included stands dominated by *Q. robur* and *Q. petraea*, mainly *Galio sylvatici-Carpinetum* Oberd. 1957 and secondary oak forests on nutrient-rich soils, including luvisols, cambisols, and gleysols. All

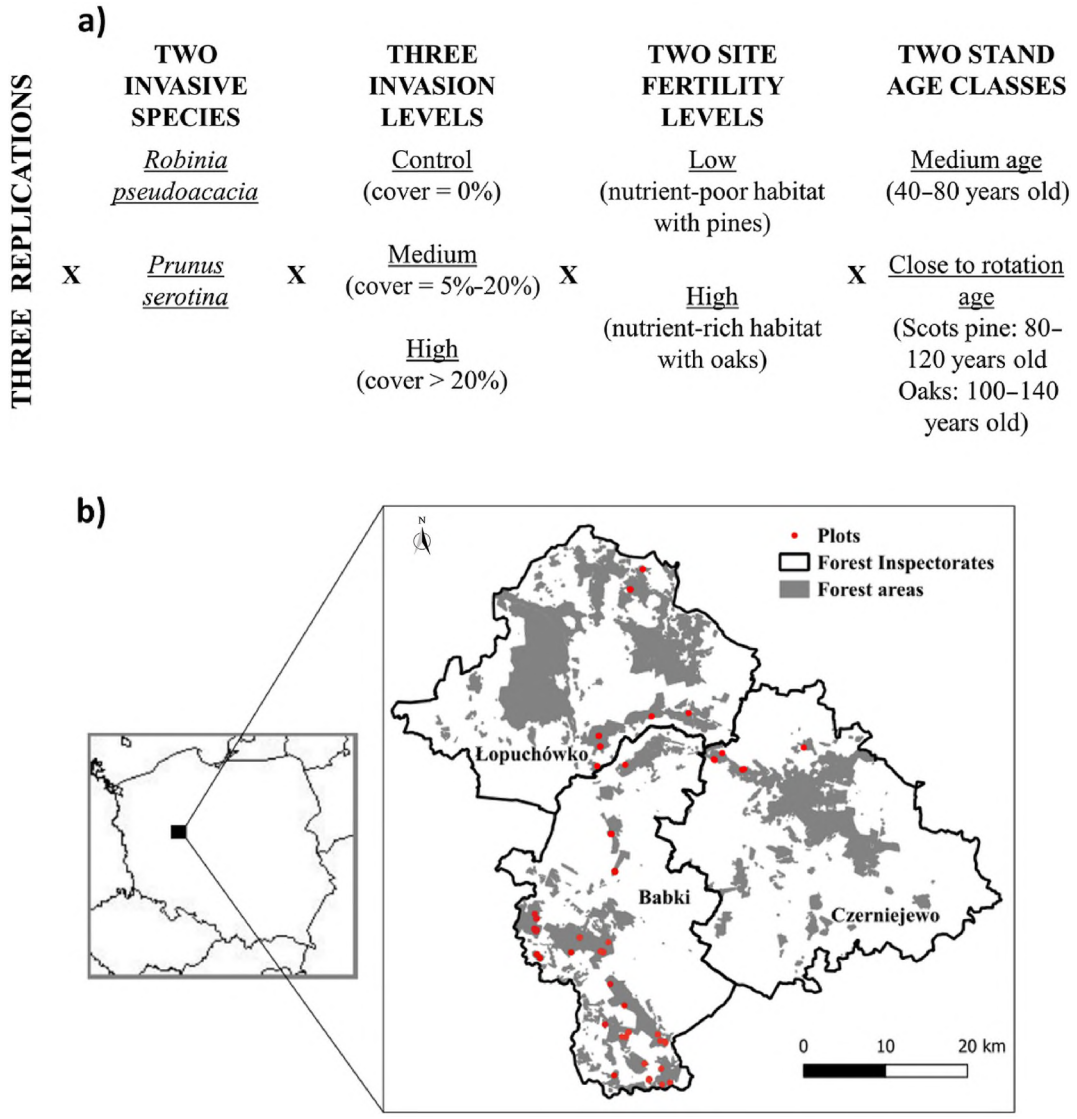

Fig. 1. Scheme of the study design, including stand features analyzed in each plot (a) and distribution of study plots (n = 72) in Poland within three forest inspectorates: Babki, Czerniejewo, and Łopuchówko (b).

plots are managed by state forests within three inspectorates: Babki, Łopuchówko, and Czerniejewo. Geographically, all plots belong to the Greater Poland Lakeland. The region is characterized by low precipitation. The climatic conditions are similar in all three inspectorates. Mean annual precipitation reaches 500–550 mm and is lower than values for the whole country. The mean annual temperature is 8.5°C, and the mean growing season temperature is approximately 16°C (BDL, 2024).

2.3. Study design and data collection

We established 72 circular (0.05 ha) plots in managed forests in western Poland in the three forest inspectorates: Babki, Czerniejewo, and Łopuchówko (the State Forests). The area covered in our study was located between 52°06′15″ and 52°40′10″ N and 16°54′31″ and 17°21′01″ E (Fig. 1b). We selected study sites representing early and intermediate phases of colonization of native stands by the neophytes studied. Our initial intention was to find areas with different abundances of the studied invasive species. We adopted three coverage ranges, control (0%), low coverage (5%–20%), and high coverage (>20%), for further assessment of a more precise invasive species abundance gradient. However, for high coverage areas, we achieved a wide gradient of neophyte cover: up to 80% for *P. serotina* and 72% for *R. pseudoacacia* (more information in section 2.4). After measurements of diameter at breast height (DBH) we determined the quantitative gradient of the invasion, expressed in terms of biomass and share of total biomass. In addition to cover, we differentiated our plots in terms of age. We looked for stands of middle age (40–80 years old) and close to rotation age (80–120 years old for Scots pine and 100–140 years old for oaks). We also differentiated plots in terms of habitat fertility (poor sites with Scots pine and rich sites with oaks). In this way, we established 72 study plots (three replications per variant; Fig. 1a). To avoid spatial autocorrelation, we established plots of the same type separated by at least 5 km. We also ensured homogenous coverage of the studied invasive species, and selected study plots in homogenous stands, avoiding large gaps and exceptionally closed canopies. Furthermore, we tried to avoid the admixture of *R. pseudoacacia* and *P. serotina* on the selected plots to prevent masking the influence of each neophyte. Additionally, we avoided admixtures of native species, because they may have made interpretation of the results difficult and also could have masked the effects of the neophytes. In the case of coniferous forests with Scots pine, avoiding admixtures was much easier; there were only small admixtures of sessile oak *Q. petraea* or silver birch *Betula pendula*. It was more difficult to find typical oak monocultures. Admixtures with *Carpinus betulus* or *Acer pseudoplatanus* were quite common both in the canopy and subcanopy layers, but they never were as dominant as oaks. It should be also mentioned that it was not possible to avoid admixture of the studied neophytes with native species in the understory. However, this limitation applied to most plots, so it did not impair comparisons among them. Moreover, we avoided stands of trees that were heavily weakened and showed visible signs of disease and damage from pests, as these could negatively impact tree growth and mask the effects of the studied neophytes. The mean ages of stands in the control plots (84.0 ± 29.6 years) and plots with *R. pseudoacacia* (85.5 ± 23.8 years) were very similar. For *P. serotina*, we found a lower average age of stands (76.0 ± 23.8 years). The youngest specimens of *R. pseudoacacia* and *P. serotina* observed on our plots were 4–5 years old. The oldest recorded specimens were approximately 40 years old for *P. serotina* and approximately 79 years old for *R. pseudoacacia*, according to radial rings from wood core samples collected in the field (unpublished data).

In September of 2021 and 2022, we measured the DBH of all of the living specimens of each species that were >1.3 m tall. We used these measurements to calculate the total aboveground biomass, the absolute invasive species biomass, and the proportion of total aboveground biomass accounted for by invasive species. In January 2023, we used a Haglöf increment borer to collect wood core samples at a height of 1.3 m from five trees per plot (pines or oaks) facing two directions (north and east). We sampled only dominant trees. It certainly would have been interesting to also examine the impact on pines and oaks growing in the lower levels of the stand. However, in many of our plots, we did not observe pine or oak trees in the lower forest strata. In particular, pine and young oak stands were quite uniform in terms of DBH distributions. Moreover, many studies examining tree growth sampling mainly dominant trees (Thurm and Pretzsch, 2016; Steckel, M. et al., 2020; Ruiz-Peinado et al., 2021; Vospernik et al., 2023) as they show stronger responses to competitive conditions or disturbances. When selecting trees to sample to determine the distribution of the DBH of the dominant tree in the area, we focused on the health and condition of the individuals. Since we did not define the competition conditions separately for each sample tree, we ensured that the cover of invasive species was evenly dispersed within plots and their surroundings by establishing study plots within homogenous forest patches. In total, we collected 720 wood core samples. The core increment samples were sanded and then scanned at 1,200 dpi resolution. We used CooRecorder and CDendro (Cybis software) to measure average annual growth of studied native trees on each plot over the last five years (2018–2022) and to cross-validate samples for the same trees. During data processing, we rejected three oaks and three pines from formal analysis due to poor visibility of annual rings after preparation or serious damage or defects in samples that could have negatively affected the precision of measurements.

2.4. Defining the invasion gradient

To define different metrics of species abundance, we used DBH measurements to calculate the basal area, density, and aboveground biomass of the studied species. Moreover, we calculated the stand aboveground biomass to express the proportion accounted for by the studied species. The aboveground biomass for each of the species within the plots was calculated using the allometric equations published in different studies (Alberti et al., 2005; Brown, 1976; Forrester et al., 2017; Jagodziński et al., 2018, 2019; Zasada, 2017). We assigned species not assessed by these authors to other generic groups (see Tables S1 and S2 for details). Then, we calculated the proportion of total aboveground biomass accounted for by *P. serotina* and *R. pseudoacacia* for each study plot (invader proportion).

The abundance of trees in an ecosystem can be determined in many ways. In our study, canopy cover helped us differentiate the invasion gradient during the selection of study plots before their establishment. For each area, we estimated the canopy cover as precisely as possible, however, canopy cover do not fully capture differences when comparing *P. serotina* and *R. pseudoacacia* (Fig. 2) and not fully describe particular phase of the invasion. Biomass that we used for invasion gradient was calculated using a detailed measurements of DBH. For that reason, we decided to use the proportion of total aboveground biomass accounted for by invasive species and invasive species absolute aboveground biomass as independent variables in our models. In the results section (Fig. 2), we showed how other quantitative indicators, including canopy cover, depend on the proportion of the invasive species in the total aboveground biomass. Typically, it was not difficult to find *P. serotina* stands in the early stages of invasion, so we dedicated substantial effort to looking for stands with larger *P. serotina* trees. A much larger problem was finding pine or oak stands with *R. pseudoacacia* and without a large proportion of *P. serotina*. Both of these mentioned limitations affected the final gradient we achieved, which was generally low for *P. serotina* and was hardly representative for *R. pseudoacacia*, which had a larger gradient.

2.5. Data analyses

All analyses were conducted using R software (R Core Team, 2023). All data are available in the figshare repository (Dyderski and Bury, 2024). In our study we included the aboveground biomass of sample

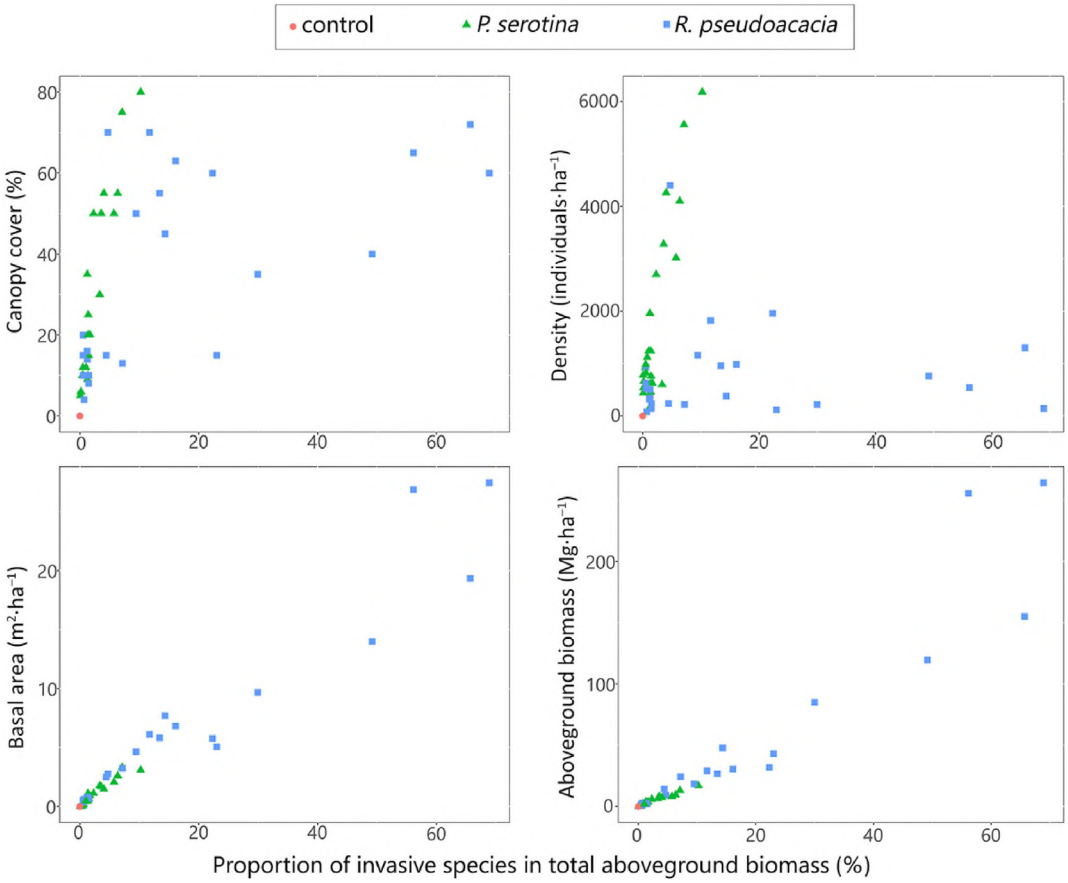

Fig. 2. Scatterplots of the proportion of total aboveground biomass accounted for by invasive species (%) and four different invasive species quantitative gradient indicators: canopy cover (%), density (ind.·ha^{-1}), basal area (m^2·ha^{-1}), and aboveground biomass (Mg·ha^{-1}). The colors and shapes of the points are explained above the graphs. The control consisted of all plots with no studied neophytes (n = 24).

trees after late (summer) growth in 2017 (or before early (spring) growth in 2018), designated AB_{2018}, and after late (summer) growth in 2022, designated AB_{2022}. This period is hereafter referred to as the period from 2018 to 2022. The difference in the biomass of pines and oaks between 2018 and 2022, relative to the biomass in 2022 (relative aboveground biomass increment, relABinc), was calculated at the tree level and at the stand level. We calculated relABinc as:

$$\text{relABinc} = \frac{AB_{2022} - AB_{2018}}{AB_{2022}}$$

where relABinc is the relative aboveground biomass increment (dimensionless), AB_{2022} is the aboveground biomass of individual pines/oaks in 2022 (Mg), and AB_{2018} is the aboveground biomass of individual pines/oaks in 2018 (Mg).

At the stand level, the growth of the remaining trees from which no core samples were taken was estimated based on the growth of the sample trees and their DBH. Finally, the relative increase in biomass for pines and oaks at the stand level was calculated from the sum of the aboveground biomass of all pines and oaks and the sum of their increments using a formula analogous to that for relABinc for individual trees.

The impacts of the studied neophytes were analyzed separately on the tree level and on the stand level and separately for stands with oaks and pines. For the tree level, we used generalized linear mixed-effects models (GLMMs) assuming a beta distribution of the dependent variable. GLMMs at the tree level included DBH of individual trees, proportion of neophytes, and their interaction as fixed effects and plot ID as a random effect. At the stand level, we used generalized linear models (GLMs) assuming a beta distribution of the dependent variable, including stand age, neophyte proportion, and their interaction as predictors. These models assessed the independence of particular observations aggregated on studied plots. For visualization of interactions, we used the "ggpredict" function from the "ggeffects" package (Lüdecke, 2018) and adopted thresholds adjusted to the width of the quantitative gradient of both neophytes: for *R. pseudoacacia*, 0%, 10%, 25%, and 50%, and, for *P. serotina*, 0%, 2.5%, 5%, and 8%. This function provides marginal responses, that is, a mean predicted outcome for the general population (excluding random effects) assuming all other predictors are at a constant (mean) level. We used the Akaike information criterion (AIC) to choose the best models (those with the lowest AIC value). We used the "dredge" function from the "MuMIn" package (Bartoń, 2023) for model selection and calculation of AICc (AIC corrected for small sample size). We used the "ggplot2" package (Wickham, 2016) to produce graphs presenting the results.

3. Results

Within 72 plots, we recorded 41 different woody species. The age of the dominant species (Scots pine or oaks), determined based on information available in the Forest Data Bank (BDL, 2024) and measurements taken in the main stands, ranged from 44 to 139 years old with an average of 81.8 ± 27.9. Observed total aboveground biomass on the plots varied from 143.2 to 507.9 Mg·ha^{-1} with an average of 234.3 ± 83.7 Mg·ha^{-1}. The DBH of the sampled oaks ranged from 21 to 80 cm with an average of 43 ± 12 cm. The DBH of the sampled pines ranged from 20 to 49 cm with an average of 30 ± 4 cm (Fig. S1).

For different quantitative indicators, we obtained slightly different gradients. The canopy cover of *P. serotina* ranged from 5% to 80% with an

average of 27.8% ± 23.1%. For *R. pseudoacacia*, canopy cover had a similar range, from 4% to 72% with an average of 34.8% ± 24.5%. However, if we considered the number of individuals, basal area, and aboveground biomass, the differences were much more distinct. The density of *P. serotina* ranged from 180 to 6,180 ind.·ha^{-1} with an average of 1,793 ± 1,722 ind.·ha^{-1}. The density of *R. pseudoacacia* ranged from 80 to 4,400 ind.·ha^{-1} with an average of 789 ± 928 ind.·ha^{-1}. The average basal area for *P. serotina* ranged from 0.01 to 3.30 m^2·ha^{-1} with an average of 0.98 ± 0.10 m^2·ha^{-1}, while for *R. pseudoacacia* it ranged from 0.35 to 27.47 m^2·ha^{-1} with an average of 6.38 ± 7.93 m^2·ha^{-1}. Aboveground biomass of *P. serotina* ranged from 0.18 to 17.03 Mg·ha^{-1} with an average of 4.39 ± 4.34 Mg·ha^{-1}. For *R. pseudoacacia*, aboveground biomass ranged from 0.83 to 264.45 Mg·ha^{-1} with an average of 48.86 ± 75.90 Mg·ha^{-1} (Fig. 2).

The proportion of total aboveground biomass accounted for by invasive species ranged from 0.1% to 10.2% for *P. serotina* (0.1%–10.2% in oak stands and 0.1%–7.1% in Scots pine stands) with an average of 2.3% ± 2.6% (1.9% ± 2.8% in oak stands, 2.8% ± 2.5% in pine stands). For *R. pseudoacacia*, this proportion ranged from 0.5% to 68.9% (0.5%–68.9% in oak stands, 0.6%–65.7% in pine stands) with an average of 16.9% ± 21.6% (21.3% ± 24.4% in oak stands, 12.4% ± 18.2% in pine stands) (Table 1, Fig. 3).

3.1. Effects of Robinia pseudoacacia

3.1.1. Individual tree level

At the tree level, we did not find a statistically or biologically significant impact of *R. pseudoacacia* on native trees' relative increments of aboveground biomass. We observed a small but statistically nonsignificant decrease in relABinc with the increasing quantitative invasion gradient of black locust. Neither the age of the trees nor the proportion of invaders in the stand had any effect on the growth of pines or oaks. For oaks with 30-cm DBH, relABinc decreased from 0.18 in control stands to 0.15 in stands with 50% *R. pseudoacacia*. For oaks with 50-cm DBH, relABinc decreased from 0.14 in control stands to 0.12 in stands with 50% *R. pseudoacacia*. For oaks with 70-cm DBH, relABinc decreased from 0.11 in control stands to 0.10 in stands with 50% *R. pseudoacacia*. For Scots pines with 20-cm DBH, we observed the same relABinc values, 0.15, in control stands and stands with 50% *R. pseudoacacia*. For Scots pines with 30-cm DBH, relABinc decreased from 0.16 in control stands to 0.14 in stands with 50% *R. pseudoacacia*. For Scots pines with 40-cm DBH, relABinc decreased from 0.17 in control stands to 0.13 in stands with 50% *R. pseudoacacia*. However, these results require cautious interpretation, as *R. pseudoacacia* reached a proportion of stand biomass ≥50% in only four study plots (Fig. 4, Table 2).

3.1.2. Stand level

At the stand level, we did not find a statistically or biologically significant impact of *R. pseudoacacia* on native trees' relative increments of aboveground biomass. In the oak and pine stands, we observed a decreasing trend in relative annual biomass increment with an increase in the quantitative gradient of *R. pseudoacacia*. Neither an increase nor decrease was observed in 120-year-old oak stands. In 50-year-old pine stands, relABinc decreased from 0.24 in control stands to 0.23 in stands with 50% *R. pseudoacacia*. In 50-year-old oak stands, relABinc decreased from 0.42 in control stands to 0.41 in stands with 50% *R. pseudoacacia*. In 80-year-old pine stands, relABinc decreased from 0.16 in control stands to 0.11 in stands with 50% *R. pseudoacacia*. In 80-year-old oak stands, relABinc decreased from 0.42 in control stands to 0.41 in stands with 50% *R. pseudoacacia*. In 120-year-old pine stands, relABinc decreased from 0.10 in control stands to 0.03 in stands with 50% *R. pseudoacacia*. In 120-year-old oak stands, relABinc reached 0.41 and did not change along the *R. pseudoacacia* biomass proportion gradient. The stand age was a statistically significant predictor of relABinc for pines ($p < 0.001$) but not for oaks ($p = 0.149$). However, these results also require caution in interpretation, as *R. pseudoacacia* reached a proportion of stand biomass ≥50% in only four study plots (Fig. 4, Table 2).

3.2. Effects of Prunus serotina

3.2.1. Individual tree level

At the tree level, we did not find a statistically or biologically significant impact of *P. serotina* on native trees' relative increments of aboveground biomass. For oaks with 30-cm DBH, relABinc decreased from 0.19 in control stands to 0.17 in stands with 8% *P. serotina*. For oaks with 50-cm DBH, relABinc decreased from 0.16 in control stands to 0.09 in stands with 8% *P. serotina*. For oaks with 70-cm DBH, relABinc decreased from 0.14 in control stands to 0.04 in stands with 8% *P. serotina*. For pines with 20-cm DBH, relABinc decreased from 0.21 in control stands to 0.18 in stands with 8% *P. serotina*. For pines with 30-cm DBH, relABinc increased from 0.17 in control stands to 0.20 in stands with 8% *P. serotina*. For pines with 40-cm DBH, relABinc increased from 0.14 in control stands to 0.23 in stands with 8% *P. serotina*. It is important to emphasize that none of these results were statistically significant. DBH was a statistically significant predictor of relABinc for oaks ($p = 0.026$) but not for pines ($p = 0.139$) (Fig. 5, Table 3).

3.2.2. Stand level

At the stand level, we did not find a statistically or biologically significant impact of *P. serotina* on native trees' relative increments of aboveground biomass. In 50-year-old pine stands, relABinc increased from 0.21 in control stands to 0.32 in stands with 8% *P. serotina*. In 50-year-old oak stands, relABinc decreased from 0.43 in control stands to 0.42 in stands with 8% *P. serotina*. In 80-year-old pine stands, relABinc increased from 0.18 in control stands to 0.22 in stands with 8% *P. serotina*. In 80-year-old oak stands, relABinc decreased from 0.42 in control stands to 0.39 in stands with 8% *P. serotina*. In 120-year-old pine stands, relABinc decreased from 0.14 in control stands to 0.13 in stands with 8% *P. serotina*. In 120-year-old oak stands, relABinc decreased from 0.42 in control stands to 0.35 in stands with 8% *P. serotina*. The stand age

Table 1
Basic characteristics of study plots of different types (**control**: control plots; **P. ser**: plots with *P. serotina*; **R. pse**: plots with *R. pseudoacacia*; **oak**: plots with oaks *Q. robur* and *Q. petraea* dominating the main stands; **pine**: plots with Scots pine *P. sylvestris* dominating the main stands; **Total AB**: total aboveground biomass).

	Proportion of invader (%)				Stand age (years)				Total AB (Mg·ha^{-1})			
	Min.	Mean	SD	Max.	Min.	Mean	SD	Max.	Min.	Mean	SD	Max.
control	0.0	0.0	0.00	0.0	47	84.0	29.63	139	143.7	240.2	97.75	507.9
oak	0.0	0.0	0.00	0.0	47	94.0	33.88	139	162.7	292.0	113.82	507.9
pine	0.0	0.0	0.00	0.0	50	74.1	21.73	117	143.7	188.5	34.38	254.3
P. ser	0.1	2.3	2.62	10.2	44	76.0	23.75	129	143.2	209.4	41.42	287.5
oak	0.1	1.9	2.80	10.2	44	84.7	24.84	129	152.2	221.8	46.92	287.5
pine	0.1	2.8	2.46	7.1	45	67.3	19.95	98	143.2	197.1	32.43	234.2
R. pse	0.5	16.9	21.56	68.9	54	85.5	29.97	139	143.2	253.3	96.50	456.6
oak	0.5	21.3	24.42	68.9	54	94.7	33.16	139	160.2	310.4	105.75	456.6
pine	0.6	12.4	18.22	65.7	54	76.3	24.39	117	143.2	196.2	34.30	250.2
All plots	0.0	6.4	14.47	68.9	44	81.8	27.85	139	143.2	234.3	83.73	507.9

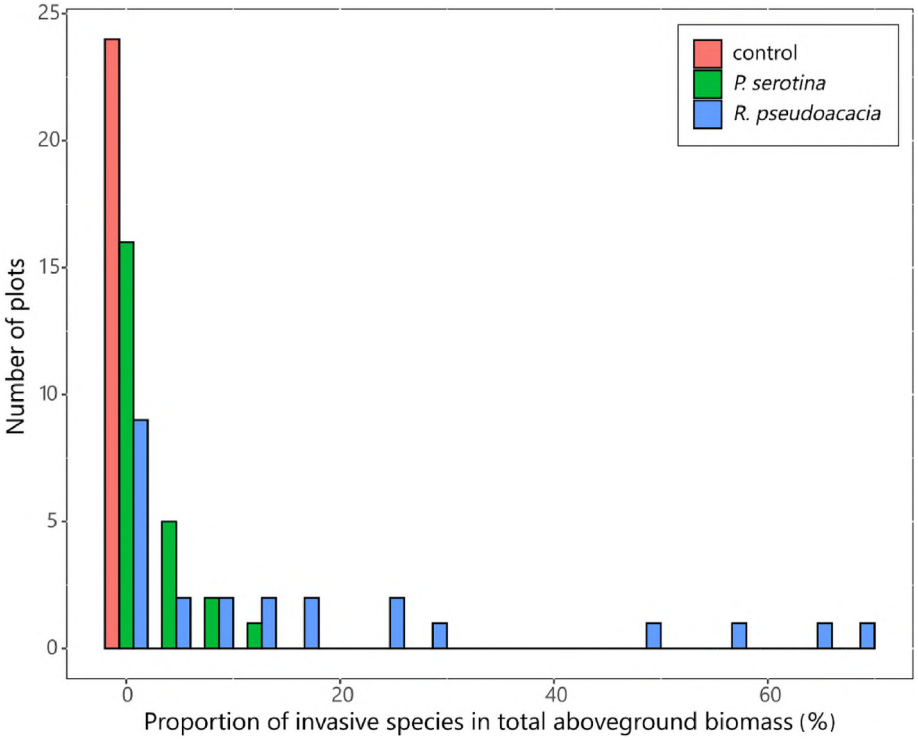

Fig. 3. The number of plots of each type with various proportions of total aboveground biomass accounted for by invasive trees (%) (control: $n = 24$ plots; *R. pseudoacacia*: $n = 24$ plots; *P. serotina*: $n = 24$ plots).

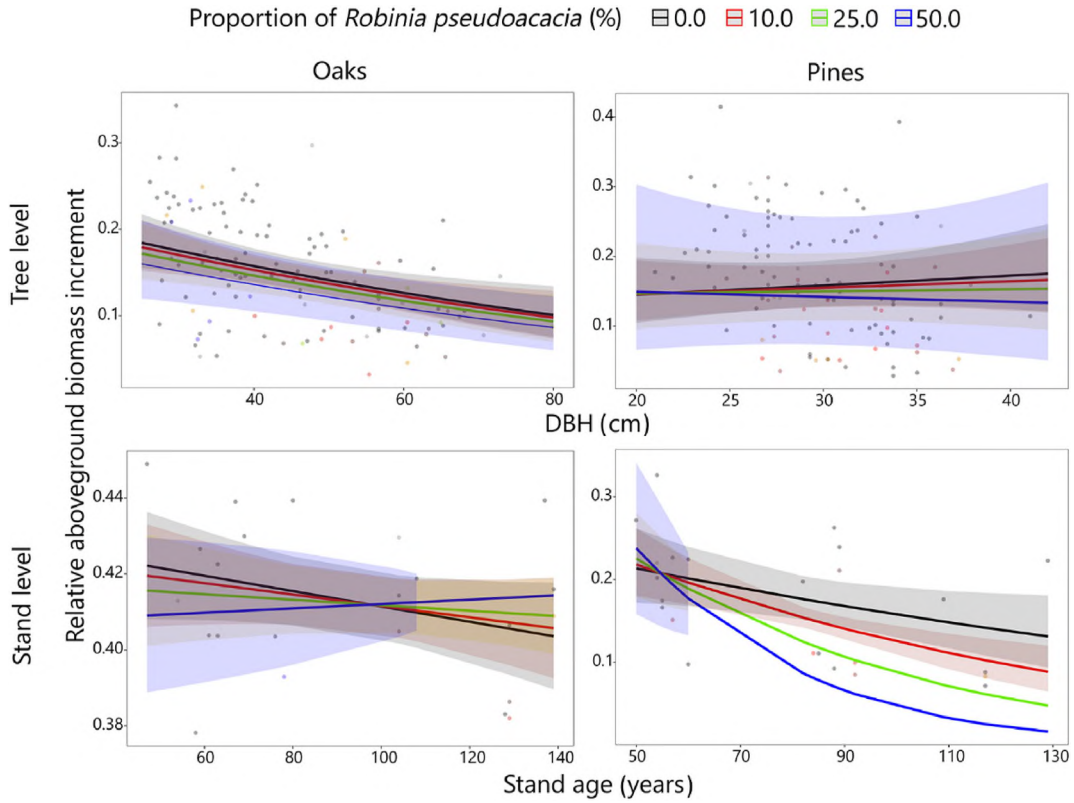

Fig. 4. Generalized linear mixed-effects models (beta distribution) for relative aboveground biomass increment depending on diameter at breast height and *R. pseudoacacia* abundance gradient at the tree level. Generalized linear models (beta distribution) for relative aboveground biomass increment depending on stand age and *R. pseudoacacia* abundance gradient at the stand level.

Table 2
Generalized linear mixed-effects models (beta distribution) for relative aboveground biomass increment at the tree level and generalized linear models (beta distribution) at the stand level along an *R. pseudoacacia* abundance gradient.

	Robinia pseudoacacia				
	Variable	Estimate	SE	*z*	*p*
Tree level:					
Oak	(Intercept)	−0.9993	0.2192	−4.56	<0.001
plots = 24	DBH	−0.0167	0.0048	−3.47	<0.001
obs. = 118	Invader proportion	−0.0148	0.0086	−1.72	0.086
$AICc_0 = -361.3$	DBH × Invader proportion	0.0003	0.0002	1.44	0.149
AICc = −361.8					
$\sigma^2 = 0.06686$					
$\sigma = 0.2586$					
Pine	(Intercept)	−1.9762	0.4577	−4.32	<0.001
plots = 24	DBH	0.0102	0.0148	0.69	0.491
obs. = 117	Invader proportion	0.0071	0.0213	0.33	0.740
$AICc_0 = -318.3$	DBH × Invader proportion	−0.0003	0.0007	−0.47	0.636
AICc = −323.5					
$\sigma^2 = 0.2784$					
$\sigma = 0.5276$					
Stand level:					
Oak	(Intercept)	−0.2747	0.0556	−4.945	<0.001
obs. = 24	Stand age	−0.0008	0.0006	−1.443	0.149
$AICc_0 = -107.8$	Invader proportion	−0.0021	0.0030	−0.703	0.482
AICc = −111.1	Stand age × Invader proportion	0.0000	0.0000	0.640	0.522
Pine	(Intercept)	−0.3898	0.2731	−1.427	0.154
obs. = 24	Stand age	−0.0155	0.0038	−4.124	<0.001
$AICc_0 = -70.9$	Invader proportion	0.0145	0.0219	0.660	0.509
AICc = −72.5	Stand age × Invader proportion	−0.0003	0.0004	−0.825	0.410

Abbreviations: SE: standard error; *z*: test statistic; *p*: *p*-value; obs.: number of observations; AICc: Akaike information criterion, corrected for small sample size; $AICc_0$: AICc of null model (intercept and random effects only); σ: variance of random effects; σ^2: standard deviation of random effects.

was a statistically significant predictor of relABinc for pines ($p < 0.001$) but not for oaks ($p = 0.152$) (Fig. 5, Table 3).

3.3. Effect based on absolute invasive species biomass: alternative analysis

We conducted analogous analyses for the absolute value of invader biomass, which revealed similar trends, with small exceptions: DBH was a statistically significant predictor of relABinc in oak stands with *R. pseudoacacia* ($p < 0.01$) and *P. serotina* ($p < 0.01$), and *P. serotina* aboveground biomass was statistically significant predictor of relABinc in oak stands ($p = 0.03$). However, despite statistical significance, the effect sizes were small and biologically irrelevant (Table S3).

4. Discussion

4.1. Effect of species admixtures

Studies of species-mixing effects are extremely important in the context of climate change (Motte et al., 2023; Reyer et al., 2010; Steckel et al., 2020). The principle of complementarity in resource use, along with differences in the biology and ecology of individual species, is considered crucial (Pretzsch, 2009; Pretzsch and Forrester, 2017). The productivity of both Scots pine and oaks in monocultures versus mixed stands has been studied. Mixing of Scots pine and oak *Q. petraea/Q. robur* was studied by Pretzsch et al. (2020) on 36 triplets in 13 countries in Europe. The average standing stem volume was 436 $m^3 \cdot ha^{-1}$ for pine monocultures, 360 $m^3 \cdot ha^{-1}$ for oak monocultures, and 418 $m^3 \cdot ha^{-1}$ for mixed stands. The periodical annual volume increment were 10.5 $m^3 \cdot ha^{-1} \cdot year^{-1}$ for pine monocultures, 9.1 $m^3 \cdot ha^{-1} \cdot year^{-1}$ for oak monocultures, and 10.5 $m^3 \cdot ha^{-1} \cdot year^{-1}$ for mixed stands. Basal area and volume increments of *P. sylvestris* were 9% higher in mixed stands than in monocultures. In our study, the mean total aboveground biomass in oak stands was lower (−32%) with *P. serotina* and higher (+6%) with *R. pseudoacacia* than in control plots with oaks. The mean total aboveground biomass in pine stands was higher with *P. serotina* (+4%) and with *R. pseudoacacia* (+4%) than in control plots with Scots pine (Table 1). Vospernik et al. (2023) showed that mixed stands of Scots pine and oak *Q. robur/Q. petraea* demonstrated a positive impact on tree growth, but the mixing effects were significant only for pines. In a different study (Del Río et al., 2017), mixed stands of Scots pine and European beech *Fagus sylvatica* L. showed advantages in stem base growth at the community level (temporal stability of the basal area increment was on average 15% lower in the monoculture than in the mixed stands; for beeches, it was 17% lower in pure stands than in the mixed stands; for pines, it was 13% lower). At the population level, no significant changes were observed, but species-specific effects were significant. For pines, the mean and standard deviation were lower in mixed stands (21%) than in pure stands (27%). For beeches, the mean and standard deviation were higher in mixed stands (56%) than in pure stands (41%). On the level of individual trees, no statistically important effect of mixing was observed (Del Río et al., 2017). Mixed stands of Scots pine and spruce *Picea abies* had higher diversity in stand height, with better results for mixed stands, particularly for Scots pines (17% higher basal area, 25% higher standing volume), while spruce showed a statistically nonsignificant low negative effect (Ruiz-Peinado et al., 2021). Oaks have also been studied in the context of mixed forests. In the conditions of central Belgium, *F. sylvatica* may have higher radial growth, but that of *Q. robur* is lower than in monocultures (Vannoppen et al., 2019). In our study, we did not observe a significant effect of *P. serotina* or *R. pseudoacacia* on the aboveground biomass increments of native *P. sylvestris*, *Q. robur*, or *Q. petraea*, either at the individual tree or stand level. However, the above examples show that the species-mixing effect can be specific to particular pairs of species, so it is worth studying more intensively.

A dominant tree's ability to efficiently acquire resources may be more critical for its growth than competition from neighbors (D'Amato and Puattmann, 2004; Kubota and Hara, 1995; McLellan et al., 1997; Wagner and Radosevich, 1998). The relative dominance hypothesis suggests that competition intensity depends on the relative abundance of interacting species. The more a species dominates a stand, the lower the competition from other species with a smaller share (D'Amato and Puattmann, 2004). This might explain why mixed stands of *R. pseudoacacia* (*P. serotina*)–pine or black locust *R. pseudoacacia* (*P. serotina*)–oak did not differ significantly from pure stands. Our results suggest that facilitation and competition between invasive and native species complemented each other within our study plots. Intraspecific competition for light, water, and nutrients among oaks/pines was not significantly higher or lower than interspecific competition in mixed stands of these species with *R. pseudoacacia* or *P. serotina*. Moreover, the presence of *R. pseudoacacia* and *P. serotina* in the understory did not restrict access to available water—unlike in a study by Giuggiola et al. (2018)—for pines or oaks in the main stand and did not significantly affect aboveground biomass increments. Evidently, the nutrient fertilization effect, along with the effect of increased decomposition of nutrient-rich litterfall (Aerts et al., 2017; Horodecki et al., 2019), was not strong enough to be observed in annual growth increments.

4.2. Effect of Robinia pseudoacacia

Of particular interest is *R. pseudoacacia*, known for its nitrogen-fixing ability and competitive advantage in temperate climates, which allow it to act as an effective transformer in forest ecosystems (Aerts et al., 2017; Cierjacks et al., 2013). The transformation and impact of mature

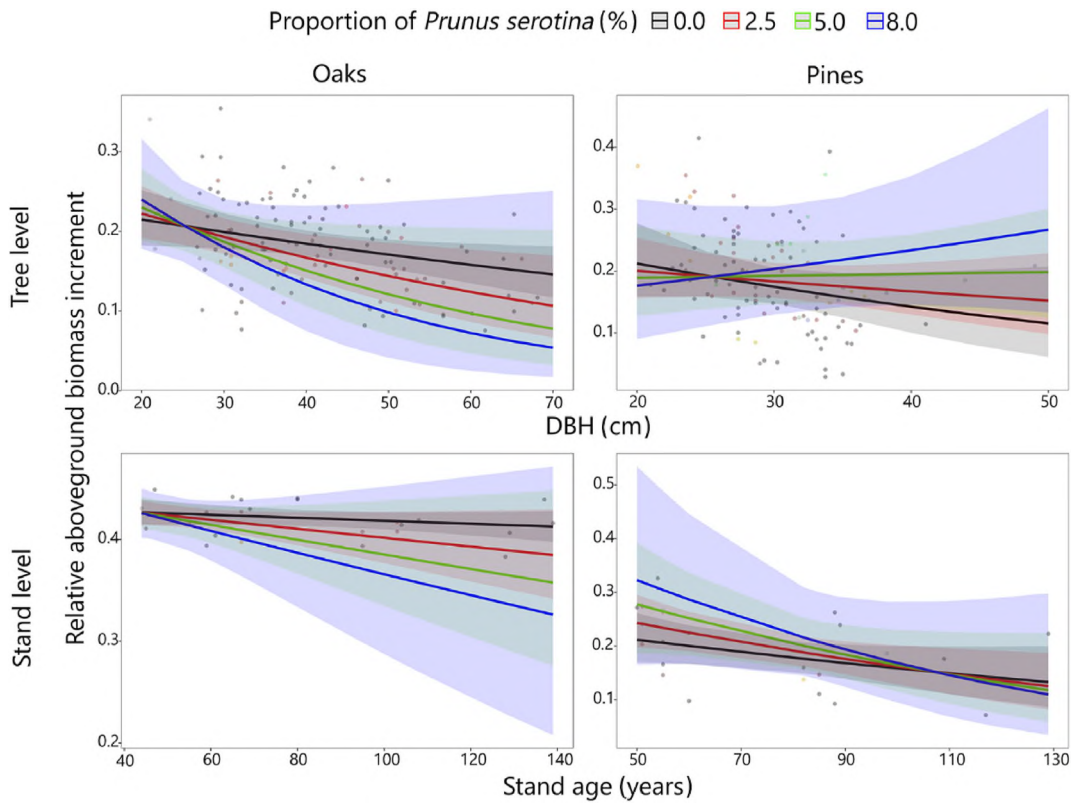

Fig. 5. Generalized linear mixed-effects models (beta distribution) for relative aboveground biomass increment depending on diameter at breast height and *P. serotina* abundance gradient at the tree level. Generalized linear models (beta distribution) for relative aboveground biomass increment depending on stand age and *P. serotina* abundance gradient at the stand level.

R. pseudoacacia trees in native stands may affect the crown zone, modifying light conditions and increasing space for the crown expansion of other species (Dyderski and Jagodziński, 2019). Effects on soil properties, pH, nutrient uptake, and organic matter deposition also play a role, influencing litter decomposition rates (Horodecki et al., 2019) and indirectly impacting soil biota (Slabejová et al., 2023). The loosening of the canopy by black locust is particularly significant in May, when native species like oaks are already leafed out while black locust is not. This may have a greater impact on oaks, which experience intensive radial growth in May (Puchałka et al., 2017). However, this might be less relevant for pine, which exhibits the most substantial radial growth in June. Pine and oak trees grow slightly differently throughout the year. According to Topcuoglu (1940), for pine, the most intensive growth occurs in June and accounts for 58% of annual growth. For oak, growth lasts from May to August and is fairly evenly distributed over the first three months. A study assessing the cambial activity of *Q. petraea* revealed that the onset of cambial activity is in March and the end is in August (Puchałka et al., 2024). Growth depends on water availability in the soil, which is limited by interception loss. A study in China (Ma et al., 2019) suggested that *R. pseudoacacia* has a smaller impact on interception loss but higher free throughfall and stemflow compared to *Pinus tabuliformis*. This interception loss phenomenon affects forest water conditions. Li et al. (2021) demonstrated that *R. pseudoacacia* expansion leads to modifications of the physical and chemical properties of soil, influencing soil nutrient availability, water properties, and soil structure. However, another study by the same author indicated that the coppicing of *R. pseudoacacia* has negative effects on soil compared to stands grown from seedlings (Li et al., 2022). Qiu et al. (2010) highlighted an increase in organic carbon, nitrogen, and certain enzymes in *Robinia*-inhabited stands, suggesting an age-dependent impact of *R. pseudoacacia* on soil properties—an aspect crucial for the hypothesized *per capita* effect discussed in this study.

4.3. Effect of Prunus serotina

In our study, *P. serotina* appeared in the understory layer. For that reason, we did not observe effects on light conditions that could have affected the crown development of *P. sylvestris*, *Q. robur*, or *Q. petraea* in the main stand. However, we anticipated that the influence on the soil and the alteration of chemical element circulation would have a stimulating effect on the main stands, with a more pronounced effect expected in nutrient-poor habitats with pine. Aerts et al. (2017) suggested that black cherry alters nutrient circulation in colonized stands to its advantage. In the case of pine, they found that the phosphorus content increased by 12.3% compared to stands not inhabited by this species. Furthermore, the authors hypothesized that *P. serotina* could influence the photosynthetic capacity of trees in the main stand, which is important in the context of climate change. It has been demonstrated that *P. serotina* can have a negative impact on growth through allelopathy (Halarewicz et al., 2021), possibly limiting natural regeneration of Scots pine. However, it is challenging to relate this to our study since we focused on mature pines.

4.4. Study limitations

The biggest challenge in our study was finding a complete set of sites that fit the intended experimental design. For that reason, we were unable to fully avoid the presence of other native species, in both the main stand and understory. However, we made every effort to minimize this mixing effect and to evenly distribute this masking effect across the entire surface area studied. Other important factors influencing biomass increments are soil fertility and water availability. We selected areas characterized by the same forest habitat type and similar soil types. Nevertheless, hypothetically, we would expect that soils formed on a

Table 3
Generalized linear mixed-effects models (beta distribution) for relative aboveground biomass increment at the tree level and generalized linear models (beta distribution) at the stand level along a *P. serotina* abundance gradient. Abbreviations are the same as in Table 2.

	Prunus serotina				
	Variable	Estimate	SE	*z*	*p*
Tree level:					
Oak	(Intercept)	−1.1642	0.1904	−6.11	<0.001
plots = 24	DBH	−0.0099	0.0044	−2.23	0.026
obs. = 119	Invader proportion	0.0882	0.0768	1.15	0.251
$AICc_0 = -373.6$	DBH × Invader proportion	−0.0035	0.0029	−1.21	0.227
AICc = −375.8					
$\sigma^2 = 0.0347$					
$\sigma = 0.1863$					
Pine	(Intercept)	−0.8282	0.4875	−1.70	0.089
plots = 24	DBH	−0.0242	0.0163	−1.48	0.139
obs. = 119	Invader proportion	−0.1333	0.1223	−1.09	0.276
$AICc_0 = -308.9$	DBH × Invader proportion	0.0052	0.0036	1.44	0.151
AICc = −311.8					
$\sigma^2 = 0.1396$					
$\sigma = 0.3736$					
Stand level:					
Oak	(Intercept)	−0.2522	0.0490	−5.150	<0.001
obs. = 24	Stand age	−0.0007	0.0005	−1.433	0.152
$AICc_0 = -120.1$	Invader proportion	0.0140	0.0196	0.714	0.475
AICc = −121.8	Stand age × Invader proportion	−0.0003	0.0004	−0.920	0.357
Pine	(Intercept)	−0.3436	0.2960	−1.161	0.246
obs. = 24	Stand age	−0.0161	0.0041	−3.943	<0.001
$AICc_0 = -68.4$	Invader proportion	−0.0204	0.1187	−0.172	0.864
AICc = −69.5	Stand age × Invader proportion	0.0007	0.0014	0.516	0.606

similar parent material would experience similar water conditions. The invasion gradient we obtained, while accounting for the proportion of *P. serotina* in the total aboveground biomass, was narrow, with a maximum proportion of 10.2%, which corresponded to a canopy cover of 80%, a density of 6,180 ind.·ha^{-1}, and an aboveground biomass of 17.03 Mg·ha^{-1}. In the case of *R. pseudoacacia*, the maximum proportion of total biomass accounted for by the biomass of the invasive species was high, at 68.9%. However, there were few similar surfaces, and there was a gap in the gradient for DBH between 30 and 45 cm. Another limitation was our determination of competitiveness based on the proportion of the total aboveground biomass accounted for by the invasive species, which was determined for the entire plot (0.05 ha), assuming an even distribution of the studied neophytes within the plots. Other studies included separate measures of competition at the tree level using competition indices. For example, Giuggiola et al. (2018) assessed the influence of the understory on trees in the main forest sample by characterizing the overstory, measuring the DBH and heights of trees, and measuring the cross-sections of understory trees thicker than 1 cm within a radius of 5 m from the sample tree. Vospernik et al. (2023) analyzed data from trees within a 7-m radius, following Biging and Dobbertin (1992, 1995). Including such metrics could help separate the effects of competition; however, we believe that, in the case of evenly distributed invasive species within plots, as well as in small study plots (0.05 ha), this effect can be negligible. It should be noted that, apart from the impact of invasive species, other important factors may have simultaneously affected the relationship between the studied neophytes and native trees. Many factors mentioned in earlier in this paper, such as the impacts of natural and artificial disturbances of various intensities, the relationship between trees at the inter- and intraspecific levels, stand structure characteristics, and environmental conditions, may overlap and mask the effect of the abundance of an invasive species. Despite efforts to minimize these effects, we could not exclude them all.

4.5. Conservation and management implications

Our results have important implications for forest and conservation management of stands in the early and intermediate phases of invasion by the species studied. First, we should consider the possible negative impacts of invasive species on biodiversity or on artificial and natural forest regeneration. Of course, we should bear in mind all the limitations of our research, which were described in the previous section. Although we did not find a significant effect of invasive species on DBH or aboveground biomass, the management of *R. pseudoacacia* and *P. serotina* still requires considerable caution. All possible scenarios should be considered, and the often surprising dynamics of forest communities, including the dynamics of invasive species, should be anticipated.

As Sádlo et al. (2017) mentioned, management of *R. pseudoacacia* is particularly difficult because this species occurs in different landscapes and because the approaches of foresters and other stakeholders differ in their aims and motivations. Management methods should be adapted to local conditions and should account for both economic and ecological aspects. These authors emphasized that large-scale control is not possible and proposed eight scenarios for different environments and primary land use goals. Some of the proposed scenarios involve greater acceptance of this species, while others include greater pressure to eliminate it. Given the aims of our study, it is interesting to focus on managed mixed *R. pseudoacacia* forest, and 10% *R. pseudoacacia* cover is the most common level of admixture (Vítková et al., 2017). In stands mixed with black locust, it is worth avoiding excessive thinning of the stands in order to prevent light from entering the forest and from facilitating the development of young black locusts, which benefit from natural disturbances (Cierjacks et al., 2013).

Nyssen and Vanhellemont (2016) discussed similar considerations for the second studied species, *P. serotina*, similarly proposing several solutions adapted to its abundance and the environmental conditions prevailing in a particular location. It is therefore critical to assess whether it is necessary to eliminate or accept an invasive species or perhaps to strengthen the natural resilience of forests in a particular site. They proposed the eradication of invasive species in stands with high conservation values and in open areas, where preserving natural vegetation, such as heathlands, is a main management aim, as well in plantations on clearcuts where we introduce light-demanding species. Accepting the presence of black cherry is recommended where it is not disturbing normal forest management and when it will be possible to obtain high-quality specimens for raw material. In the case of deciduous stands, it is worth ensuring their resistance to the development of *P. serotina* invasions, and silvicultural operations should be conducted in a manner that avoids significant dilution of the main stand and of the understory, which would cause more light to enter and thereby favor *P. serotina*. However, our conclusions focused on only one of the ecosystem services of forests; we did not account for other services or for impacts on biodiversity.

5. Conclusions

Our study assessed whether two invasive species, *R. pseudoacacia* and *P. serotina*, which differ in biology and ecology, showed a *per capita* effect on native tree growth. We did not focus on stands dominated by *R. pseudoacacia*, but we studied a wide gradient of invasion dynamics related to the phases of colonization of stands where the studied species were not introduced but spread spontaneously. We did not demonstrate any biologically or statistically significant differences in the increases in aboveground biomass of native Scots pine or oaks along the quantitative invasion gradient. These results do not support previous claims that *R. pseudoacacia* and *P. serotina* can function as growth stimulators of

native trees. We did not demonstrate a positive effect of mixing. It should be emphasized, however, that the gradients we achieved were typical for the three forest districts studied, where *P. serotina* trees had a low biomass and mature *R. pseudoacacia* stands were quite poorly represented, so we should be careful when comparing these areas with other parts of Poland or Europe. However, our results suggest that the invasive species studied will not negatively impact our native species by competing for resources such as water, nutrients, and light. Neither competition nor facilitation prevailed over the other. We provided a quantitative assessment of the impacts of invasive trees on ecosystem services, which can be included in risk assessments and conservation management plans. Moreover, by accounting for the predicted further expansion of the studied neophytes due to climate change, we can prepare for future interactions related to native tree growth.

Conflicts of interest

The authors declare no conflict of interest. The funders had no role in the design of the study; in the collection, analyses, or interpretation of data; in the writing of the manuscript; or in the decision to publish the results.

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Data accessibility statement

All data supporting the results are archived in the figshare repository (Dyderski and Bury, 2024) https://doi.org/10.6084/m9.figshare.25603110.

CRediT authorship contribution statement

Sebastian Bury: Writing – review & editing, Writing – original draft, Methodology, Investigation, Formal analysis, Conceptualization. **Marcin K. Dyderski:** Writing – review & editing, Methodology, Funding acquisition, Conceptualization.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.fecs.2024.100201.

References

Aerts, R., Ewald, M., Nicolas, M., Piat, J., Skowronek, S., Lenoir, J., Hattab, T., Garzón-López, C.X., Feilhauer, H., Schmidtlein, S., Rocchini, D., Decocq, G., Somers, B., Van De Kerchove, R., Denef, K., Honnay, O., 2017. Invasion by the alien tree *Prunus serotina* alters ecosystem functions in a temperate deciduous forest. Front. Plant Sci. 8, 179. https://doi.org/10.3389/fpls.2017.00179.

Alberti, G., Candido, P., Peressotti, A., Turco, S., Piussi, P., Zerbi, G., 2005. Aboveground biomass relationships for mixed ash (*Fraxinus excelsior* L. and *Ulmus glabra* hudson) stands in eastern prealps of friuli venezia giulia (Italy). Ann. For. Sci. 62, 831–836. https://doi.org/10.1051/forest:2005089.

Ammer, C., 2019. Diversity and forest productivity in a changing climate. New Phytol. 221, 50–66. https://doi.org/10.1111/nph.15263.

Bartoń, K., 2023. MuMIn: multi-model inference. R package version 1.47.5. https://CRAN.R-project.org/package=MuMIn. (Accessed 26 March 2024).

Bauhus, J., Forrester, D.I., Gardiner, B., Jactel, H., Vallejo, R., Pretzch, H., 2017a. Ecological stability of mixed-species forests. In: Pretzch, H., Forrester, D.I., Bauhus, J. (Eds.), Mixed-Species Forests: Ecology and Management. Springer, Berlin, pp. 337–382.

Bauhus, J., Forrester, D.I., Pretzch, H., 2017b. From observations to evidence about effects of mixed-species stands. In: Pretzch, H., Forrester, D.I., Bauhus, J. (Eds.), Mixed-Species Forests: Ecology and Management. Springer, Berlin, pp. 28–66.

Biging, G., Dobbertin, M., 1995. Evaluation of competition indices in individual tree growth models. For. Sci. 41, 360–377. https://doi.org/10.1093/forestscience/41.2.360.

BDL, 2024. Bank Danych O Lasach. https://www.bdl.lasy.gov.pl/portal/mapy-en. (Accessed 26 March 2024).

Biging, G., Dobbertin, M., 1992. A comparison of distance-dependent competition measures for height and basal area growth of individual conifer trees. For. Sci. 38, 695–720.

Binkley, D., 1992. Mixtures of N_2-fixing and non-N_2-fixing tree species. In: Cannell, M.G.R., Malcolm, D.C., Robertson, P.A. (Eds.), The Ecology of Mixed-Species Stands of Trees. Blackwell Sci. Publ, London, pp. 92–123.

Bouteiller, X.P., Bussolo, M., Ségura, R., Mariette, S., Porté, A.J., 2023. Considering both sexual and clonal reproduction could help loosen the conflict of use over *Robinia pseudoacacia*. Dendrobiology 90, 30–38. https://doi.org/10.12657/denbio.090.002.

Brown, J.K., 1976. Estimating shrub biomass from basal stem diameters. Can. J. Res. 6 (2), 153–158. https://doi.org/10.1139/x76-019.

Castro-Diez, P., Vaz, A.S., Silva, J.S., van Loo, M., Alonso, A., Aponte, C., Bayón, Á., Bellingham, P.J., Chiuffo, M.C., DiManno, N., Kahua, J., Kandert, S., La Porta, N., Marchante, H., Maule, H.G., Mayfield, M.M., Metcalfe, D., Monteverdi, M.C., Nuñez, M.A., Ostertag, R., Parker, I.M., Peltzer, D.A., Potgieter, L.J., Raymundo, M., Rayome, D., Reisman-Berman, O., Richardson, D.M., Roos, R.E., Saldaña, A., Shackleton, R.T., Torres, A., Trudgen, M., Urban, J., Vicente, J.R., Vilà, M., Ylioja, T., Zenni, R.D., Godoy, O., 2019. Global effects of non-native tree species on multiple ecosystem services. Biol. Rev. 94, 1477–1501. https://doi.org/10.1111/brv.12511.

Chmura, D., 2004. Penetration and naturalisation of invasive alien plant species (neophytes) in woodlands of the Silesian Upland (Southern Poland). Nat. Conserv. 60, 3–11.

Cierjacks, A., Kowarik, I., Joshi, J., Hempel, S., Ristow, M., Von Der Lippe, M., Weber, E., 2013. Biological flora of the British isles: *Robinia pseudoacacia*. J. Ecol. 101, 1623–1640. https://doi.org/10.1111/1365-2745.12162.

Czortek, P., Królak, E., Borkowska, L., Bielecka, A., 2023. Effects of surrounding landscape on the performance of *Solidago canadensis* L. and plant functional diversity on heavily invaded post-agricultural wastelands. Biol. Invasions 25, 2477–2494. https://doi.org/10.1007/s10530-023-03050-2.

D'Amato, A.W., Puattmann, K.J., 2004. The relative dominance hypothesis explains interaction dynamics in mixed species *Alnus rubra/Pseudotsuga menziesii* stands. J. Ecol. 92, 450–463. https://doi.org/10.1111/j.0022-0477.2004.00888.x.

Del Río, M., Pretzsch, H., Ruíz-Peinado, R., Ampoorter, E., Annighöfer, P., Barbeito, I., Bielak, K., Brazaitis, G., Coll, L., Drössler, L., Fabrika, M., Forrester, D.I., Heym, M., Hurt, V., Kurylyak, V., Löf, M., Lombardi, F., Madrickiene, E., Matović, B., Mohren, F., Motta, R., Den Ouden, J., Pach, M., Ponette, Q., Schütze, G., Skrzyszewski, J., Sramek, V., Sterba, H., Stojanović, D., Svoboda, M., Zlatanov, T.M., Bravo-Oviedo, A., 2017. Species interactions increase the temporal stability of community productivity in *Pinus sylvestris–Fagus sylvatica* mixtures across Europe. J. Ecol. 105, 1032–1043. https://doi.org/10.1111/1365-2745.12727.

Dukes, J.S., Mooney, H.A., 1999. Does global change increase the success of biological invaders? Trends Ecol. Evol. 14, 135–139. https://doi.org/10.1016/S0169-5347(98)01554-7.

Dyderski, M.K., Bury, S., 2024. Dataset for No effect of invasive tree species on aboveground biomass increments of oaks and pines in temperate forests. Figshare. doi:10.6084/m9.figshare.25603110.

Dyderski, M.K., Chmura, D., Dylewski, Ł., Horodecki, P., Jagodziński, A.M., Pietras, M., Robakowski, P., Woziwoda, B., 2020. Biological flora of the British isles: *Quercus rubra*. J. Ecol. 108, 1199–1225. https://doi.org/10.1111/1365-2745.13375.

Dyderski, M.K., Jagodziński, A.M., 2019. Similar impacts of alien and native tree species on understory light availability in a temperate forest. Forests 10, 951. https://doi.org/10.3390/f10110951.

Dyderski, M.K., Paź, S., Frelich, L.E., Jagodziński, A.M., 2018. How much does climate change threaten European forest tree species distributions? Global Change Biol. 24, 1150–1163. https://doi.org/10.1111/gcb.13925.

Forrester, D.I., Bauhus, J., 2016. A review of processes behind diversity–productivity relationships in forests. Curr. For. Rep. 2, 45–61. https://doi.org/10.1007/s40725-016-0031-2.

Forrester, D.I., Tachauer, I.H.H., Annighoefer, P., Barbeito, I., Pretzsch, H., Ruiz-Peinado, R., Stark, H., Vacchiano, G., Zlatanov, T., Chakraborty, T., Saha, S., Sileshi, G.W., 2017. Generalized biomass and leaf area allometric equations for European tree species incorporating stand structure, tree age and climate. For. Ecol. Manag. 396, 160–175. https://doi.org/10.1016/j.foreco.2017.04.011.

Gams, H., 1924. Leguminosae. In: Hegi, G. (Ed.), Illustrierte Flora von Mitteleuropa, IV/3. J. Lehmanns Verlag, Munchen, Germany.

García, R.A., Fuentes-Lillo, E., Cavieres, L., Cóbar-Carranza, A.J., Davis, K.T., Naour, M., Núñez, M.A., Maxwell, B.D., Lembrechts, J.J., Pauchard, A., 2023. *Pinus contorta* alters microenvironmental conditions and reduces plant diversity in Patagonian ecosystems. Diversity 15, 320. https://doi.org/10.3390/d15030320.

Giuggiola, A., Zweifel, R., Feichtinger, L.M., Vollenweider, P., Bugmann, H., Haeni, M., Rigling, A., 2018. Competition for water in a xeric forest ecosystem – effects of understory removal on soil micro-climate, growth and physiology of dominant Scots

pine trees. For. Ecol. Manag. 409, 241–249. https://doi.org/10.1016/j.foreco.2017.11.002.
Halarewicz, A., 2011. The reasons underlying the invasion of forest communities by black cherry, *Prunus serotina* and its subsequent consequences. For. Res. Pap. 72, 267–272. https://doi.org/10.2478/v10111-011-0026-5.
Halarewicz, A., Szumny, A., Bączek, P., 2021. Effect of *Prunus serotina* Ehrh. volatile compounds on germination and seedling growth of *Pinus sylvestris* L. Forests 12, 846. https://doi.org/10.3390/f12070846.
Heger, T., Jeschke, J.M., Kollmann, J., 2021. Some reflections on current invasion science and perspectives for an exciting future. NeoBiota 68, 79–100. https://doi.org/10.3897/neobiota.68.68997.
Horodecki, P., Nowiński, M., Jagodziński, A.M., 2019. Advantages of mixed tree stands in restoration of upper soil layers on postmining sites: a five-year leaf litter decomposition experiment. Land Degrad. Dev. 30, 3–13. https://doi.org/10.1002/ldr.3194.
Huntley, J.C., 1990. Silvics of NorthNorth America. In: Burns, R.M., Honkala, B.H. (Eds.), Agriculture Handbook 654 [online]. US Department of Agriculture, Washington DC, USA.
Jactel, H., Nicoll, B.C., Branco, M., Gonzalez-Olabarria, J.R., Grodzki, W., Långström, B., Moreira, F., Netherer, S., Orazio, C., Piou, D., Santos, H., Schelhaas, M.J., Tojic, K., Vodde, F., 2009. The influences of forest stand management on biotic and abiotic risks of damage. Ann. For. Sci. 66, 701. https://doi.org/10.1051/forest/2009054, 701.
Jagodziński, A., Dyderski, M., Gęsikiewicz, K., Horodecki, P., 2018. Tree- and stand-level biomass estimation in a *Larix decidua* mill. Chronosequence. Forests 9, 587. https://doi.org/10.3390/f9100587.
Jagodziński, A.M., Dyderski, M.K., Gęsikiewicz, K., Horodecki, P., 2019. Effects of stand features on aboveground biomass and biomass conversion and expansion factors based on a *Pinus sylvestris* L. chronosequence in Western Poland. Eur. J. For. Res. 138, 673–683. https://doi.org/10.1007/s10342-019-01197-z.
Kahveci, G., Arslan, M., 2021. Factors affecting the radial growth of *Juniperus foetidissima* Willd. and *J. excelsa* M. Bieb. in central Anatolia. J. For. Sci. 67 (10), 477–488. https://doi.org/10.17221/42/2021-JFS.
Kanzler, M., Böhm, C., Freese, D., 2021. The development of soil organic carbon under young black locust (*Robinia pseudoacacia* L.) trees at a post-mining landscape in eastern Germany. New For. 52, 47–68. https://doi.org/10.1007/s11056-020-09779-1.
Knoke, T., Stimm, B., Ammer, C., Moog, M., 2005. Mixed forests reconsidered: a forest economics contribution on an ecological concept. For. Ecol. Manag. 213, 102–116. https://doi.org/10.1016/j.foreco.2005.03.043.
Korhonen, K., Stahl, G., Freudenschuss, A., Brändli, U.-B., Fridman, J., Cienciala, E., Linser, S., 2020. Criterion 1: maintenance and appropriate enhancement of forest resources and their contribution to global carbon cycles. In: State of Europe's Forests 2020, Forest Europe, pp. 30–50.
Kotta, J., 2023. Biological invasions in a changing world: introduction to the special issue. Diversity 15, 891. https://doi.org/10.3390/d15080891.
Kubota, Y., Hara, T., 1995. Tree competition and species coexistence in a sub-boreal forest, northern Japan. Ann. Bot. 76, 503–512.
Li, K., Han, X., Ni, R., Shi, G., de-Miguel, S., Li, C., Shen, W., Zhang, Y., Zhang, X., 2021. Impact of *Robinia pseudoacacia* stand conversion on soil properties and bacterial community composition in Mount Tai, China. For. Ecosyst. 8, 19. https://doi.org/10.1186/s40663-021-00296-x.
Li, K., Tian, H., Moser, W.K., Overby, S.T., Baggett, L.S., Ni, R., Li, C., Shen, W., 2022. Black locust coppice stands homogenize soil diazotrophic communities by reducing soil net nitrogen mineralization. For. Ecosyst. 9, 100025. https://doi.org/10.1016/j.fecs.2022.100025.
Liang, J., Crowther, T.W., Picard, N., Wiser, S., Zhou, M., Alberti, G., Schulze, E.-D., McGuire, A.D., Bozzato, F., Pretzsch, H., de-Miguel, S., Paquette, A., Hérault, B., Scherer-Lorenzen, M., Barrett, C.B., Glick, H.B., Hengeveld, G.M., Nabuurs, G.-J., Pfautsch, S., Viana, H., Vibrans, A.C., Ammer, C., Schall, P., Verbyla, D., Tchebakova, N., Fischer, M., Watson, J.V., Chen, H.Y.H., Lei, X., Schelhaas, M.-J., Lu, H., Gianelle, D., Parfenova, E.I., Salas, C., Lee, E., Lee, B., Kim, H.S., Bruelheide, H., Coomes, D.A., Piotto, D., Sunderland, T., Schmid, B., Gourlet-Fleury, S., Sonké, B., Tavani, R., Zhu, J., Brandl, S., Vayreda, J., Kitahara, F., Searle, E.B., Neldner, V.J., Ngugi, M.R., Baraloto, C., Frizzera, L., Bałazy, R., Oleksyn, J., Zawiła-Niedźwiecki, T., Bouriaud, O., Bussotti, F., Finér, L., Jaroszewicz, B., Jucker, T., Valladares, F., Jagodzinski, A.M., Peri, P.L., Gonmadje, C., Marthy, W., O'Brien, T., Martin, E.H., Marshall, A.R., Rovero, F., Bitariho, R., Niklaus, P.A., Alvarez-Loayza, P., Chamuya, N., Valencia, R., Mortier, F., Wortel, V., Engone-Obiang, N.L., Ferreira, L.V., Odeke, D.E., Vasquez, R.M., Lewis, S.L., Reich, P.B., 2016. Positive biodiversity-productivity relationship predominant in global forests. Science 354, aaf8957. https://doi.org/10.1126/science.aaf8957.
Lüdecke, D., 2018. ggeffects: tidy data frames of marginal effects from regression models. J. Open Source Softw. 3, 772. https://doi.org/10.21105/joss.00772.
Ma, C., Li, X., Luo, Y., Shao, M., Jia, X., 2019. The modelling of rainfall interception in growing and dormant seasons for a pine plantation and a black locust plantation in semi-arid Northwest China. J. Hydrol. 577, 123849. https://doi.org/10.1016/j.jhydrol.2019.06.021.
McLellan, A.J., Law, R., Fitter, A.H., 1997. Response of calcareous grassland plant species to diffuse competition: results from a removal experiment. J. Ecol. 85, 479. https://doi.org/10.2307/2960571.
Mina, M., Huber, M.O., Forrester, D.I., Thürig, E., Rohner, B., 2018. Multiple factors modulate tree growth complementarity in Central European mixed forests. J. Ecol. 106, 1106–1119. https://doi.org/10.1111/1365-2745.12846.
Morimoto, J., Kominami, R., Koike, T., 2010. Distribution and characteristics of the soil seed bank of the black locust (*Robinia pseudoacacia*) in a headwater basin in northern Japan. Landsc. Ecol. Eng. 6, 193–199. https://doi.org/10.1007/s11355-009-0096-1.
Motte, F., Rötzer, T., Biber, P., Uhl, E., Pritsch, K., Pretzsch, H., 2023. Growth of European beech recovered faster than that of Norway spruce after a five-year experimental drought in a mixed forest stand. Trees (Berl.) 37, 1695–1715. https://doi.org/10.1007/s00468-023-02453-x.
Namura-Ochalska, A., Borowa, B., 2015. Walka z czeremchą amerykańską *Padus serotina* (Ehrh.) Borkh. w leśnictwie Rózin w Kampinoskim Parku Narodowym; ocena skuteczności wybranych metod. In: Krzysztofiak, L., Krzysztofiak, A. (Eds.), Inwazyjne Gatunki Obcego Pochodzenia Zagrożeniem Dla Rodzimej Przyrody Red. Stowarzyszenie "Człowiek i Przyroda, Krzywe, pp. 127–142.
Nyssen, B., Vanhellemont, M., 2016. 5.6 Integrating black cherry in forest management in The Netherlands and Belgium. In: Krumm, F., Vítková, L. (Eds.), Introduced Tree Species in European Forests: Opportunities and Challenges. European Forest Institute, Freiburg, pp. 362–372. European Forest Institute.
Otręba, A., 2016. Czeremcha amerykańska *Padus serotina* (Ehrh.) borkh. In: Obidziński, A., Kołaczkowska, E., Otręba, A. (Eds.), Metody Zwalczania Obcych Gatunków Roślin Występujących Na Terenie Puszczy Kampinowskiej. Kampinowski Park Narodowy, Izabelin, pp. 73–88.
Pan, Y., Birdsey, R.A., Fang, J., Houghton, R., Kauppi, P.E., Kurz, W.A., Phillips, O.L., Shvidenko, A., Lewis, S.L., Canadell, J.G., Ciais, P., Jackson, R.B., Pacala, S.W., McGuire, A.D., Piao, S., Rautiainen, A., Sitch, S., Hayes, D., 2011. A large and persistent carbon sink in the world's forests. Science 333, 988–993. https://doi.org/10.1126/science.1201609.
Parker, I.M., Simberloff, D., Lonsdale, W.M., Goodell, K., Wonham, M., Kareiva, P.M., Williamson, M.H., Von Holle, B., Moyle, P.B., Byers, J.E., Goldwasser, L., 1999. Impact: toward a framework for understanding the ecological effects of invaders. Biol. Invasions 1, 3–19. https://doi.org/10.1023/A:1010034312781.
Pearse, I.S., Sofaer, H.R., Zaya, D.N., Spyreas, G., 2019. Non-native plants have greater impacts because of differing per-capita effects and nonlinear abundance–impact curves. Ecol. Lett. 22, 1214–1220. https://doi.org/10.1111/ele.13284.
Pretzsch, H., 2009. Forest Dynamics, Growth and Yield: from Measurement to Model. Springer Berlin Heidelberg, Berlin, Heidelberg. https://doi.org/10.1007/978-3-540-88307-4.
Pretzsch, H., Forrester, D.I., 2017. Stand dynamics of mixed-species stands compared with monocultures. In: Pretzsch, H., Forrester, D.I., Bauhus, J. (Eds.), Mixed-Species Forests: Ecology and Management. Springer, Berlin, pp. 117–209.
Pretzsch, H., Steckel, M., Heym, M., Biber, P., Ammer, C., Ehbrecht, M., Bielak, K., Bravo, F., Ordóñez, C., Collet, C., Vast, F., Drössler, L., Brazaitis, G., Godvod, K., Jansons, A., de-Dios-García, J., Löf, M., Aldea, J., Korboulewsky, N., Reventlow, D.O.J., Nothdurft, A., Engel, M., Pach, M., Skrzyszewski, J., Pardos, M., Ponette, Q., Sitko, R., Fabrika, M., Svoboda, M., Černý, J., Wolff, B., Ruíz-Peinado, R., Del Río, M., 2020. Stand growth and structure of mixed-species and monospecific stands of Scots pine (*Pinus sylvestris* L.) and oak (*Q. robur* L., *Quercus petraea* (Matt.) Liebl.) analysed along a productivity gradient through Europe. Eur. J. For. Res. 139, 349–367. https://doi.org/10.1007/s10342-019-01233-y.
Puchałka, R., Koprowski, M., Gričar, J., Przybylak, R., 2017. Does tree-ring formation follow leaf phenology in Pedunculate oak (*Quercus robur* L.)? Eur. J. For. Res. 136, 259–268. https://doi.org/10.1007/s10342-017-1026-7.
Puchałka, R., Paź-Dyderska, S., Jagodziński, A.M., Sádlo, J., Vítková, M., Klisz, M., Koniakin, S., Prokopuk, Y., Netsvetov, M., Nicolescu, V.-N., Zlatanov, T., Mionskowski, M., Dyderski, M.K., 2023. Predicted range shifts of alien tree species in Europe. Agric. For. Meteorol. 341, 109650. https://doi.org/10.1016/j.agrformet.2023.109650.
Puchałka, R., Prislan, P., Klisz, M., Koprowski, M., Gričar, J., 2024. Tree-ring formation dynamics in *Fagus sylvatica* and *Quercus petraea* in a dry and a wet year. Dendrobiology 91, 1–15. https://doi.org/10.12657/denbio.091.001.
Qiu, L., Zhang, X., Cheng, J., Yin, X., 2010. Effects of black locust (*Robinia pseudoacacia*) on soil properties in the loessial gully region of the Loess Plateau, China. Plant Soil 332, 207–217. https://doi.org/10.1007/s11104-010-0286-5.
R Core Team, 2023. R: A Language and Environment for Statistical Computing. R Foundation for Statistical Computing, Vienna.
Rebola-Lichtenberg, J., Streit, J., Schall, P., Ammer, C., Seidel, D., 2021. From facilitation to competition: the effect of black locust (*Robinia pseudoacacia* L.) on the growth performance of four poplar-hybrids (*Populus* spp.) in mixed short rotation coppice. New For. 52, 639–656. https://doi.org/10.1007/s11056-020-09813-2.
Reyer, C., Lasch, P., Mohren, G.M.J., Streck, F.J., 2010. Inter-specific competition in mixed forests of Douglas-fir (*Pseudotsuga menziesii*) and common beech (*Fagus sylvatica*) under climate change – a model-based analysis. Ann. For. Sci 67, 805. https://doi.org/10.1051/forest/2010041.
Richardson, D.M., Pysek, P., Rejmanek, M., Barbour, M.G., Panetta, F.D., West, C.J., 2000. Naturalization and invasion of alien plants: concepts and definitions. Divers. Distrib. 6, 93–107. https://doi.org/10.1046/j.1472-4642.2000.00083.x.
Röhle, H., 2018. Growth performance and management in mixed forest stands. In: Proceedings of the International Scientific Conference "Rural Development 2017.". Aleksandras Stulginskis University. https://doi.org/10.15544/RD.2017.122. Lithuania.
Ronch, F.D., Caudullo, G., de Rigo, D., 2016. *Pseudotsuga menziesii* in Europe: distribution, habitat, usage and threats. In: San-Miguel-Ayanz, J., de Rigo, D., Caudullo, G., Houston Durrant, T., Mauri, A. (Eds.), European Atlas of Forest Tree Species. Publ. Off. EU, Luxembourg, pp. 146–147.
Roy, H.E., Pauchard, A., Stoett, P., Renard Truong, T., Bacher, S., Galil, B.S., Hulme, P.E., Ikeda, T., Sankaran, K., McGeoch, M.A., Meyerson, L.A., Nuñez, M.A., Ordonez, A., Rahlao, S.J., Schwindt, E., Seebens, H., Sheppard, A.W., Vandvik, V., 2023. IPBES

Invasive Alien Species Assessment: Summary for Policymakers. Zenodo. https://doi.org/10.5281/ZENODO.7430692.
Ruiz-Benito, P., Gómez-Aparicio, L., Paquette, A., Messier, C., Kattge, J., Zavala, M.A., 2014. Diversity increases carbon storage and tree productivity in Spanish forests. Global Ecol. Biogeogr. 23, 311–322. https://doi.org/10.1111/geb.12126.
Ruiz-Peinado, R., Pretzsch, H., Löf, M., Heym, M., Bielak, K., Aldea, J., Barbeito, I., Brazaitis, G., Drössler, L., Godvod, K., Granhus, A., Holm, S.-O., Jansons, A., Makrickienė, E., Metslaid, M., Metslaid, S., Nothdurft, A., Otto Juel Reventlow, D., Sitko, R., Stankevičienė, G., Del Río, M., 2021. Mixing effects on Scots pine (*Pinus sylvestris* L.) and Norway spruce (*Picea abies* (L.) Karst.) productivity along a climatic gradient across Europe. For. Ecol. Manag. 482, 118834. https://doi.org/10.1016/j.foreco.2020.118834.
Rumyantseva, A.V., Chekrygin, S.A., Vidyagina, E.O., 2023. Interrelation of the radial increment of trees with various factors. Physiologia 3, 347–365. https://doi.org/10.3390/physiologia3020024.
Sádlo, J., Vítková, M., Pergl, J., Pyšek, P., 2017. Towards site-specific management of invasive alien trees based on the assessment of their impacts: the case of *Robinia pseudoacacia*. NeoBiota 35, 1–34. https://doi.org/10.3897/neobiota.35.11909.
Sapsford, S.J., Brandt, A.J., Davis, K.T., Peralta, G., Dickie, I.A., Gibson, R.D., Green, J.L., Hulme, P.E., Nuñez, M.A., Orwin, K.H., Pauchard, A., Wardle, D.A., Peltzer, D.A., 2020. Towards a framework for understanding the context dependence of impacts of non-native tree species. Funct. Ecol. 34, 944–955. https://doi.org/10.1111/1365-2435.13544.
Slabejová, D., Čejka, T., Hegedüšová, K., Májeková, J., Medvecká, J., Mikulová, K., Šibíková, M., Škodová, I., Šustek, Z., Jarolímek, I., 2023. Comparison of alien *Robinia pseudoacacia* stands with native forest stands across different taxonomic groups. For. Ecol. Manag. 548, 121413. https://doi.org/10.1016/j.foreco.2023.121413.
Starfinger, U., Kowarik, I., Rode, M., Schepker, H., 2003. From desirable ornamental plant to pest to accepted addition to the flora? – The perception of an alien tree species through the centuries. Biol. Invasions 5, 323–335. https://doi.org/10.1023/B:BINV.0000005573.14800.07.
Steckel, M., Del Río, M., Heym, M., Aldea, J., Bielak, K., Brazaitis, G., Černý, J., Coll, L., Collet, C., Ehbrecht, M., Jansons, A., Nothdurft, A., Pach, M., Pardos, M., Ponette, Q., Reventlow, D.O.J., Sitko, R., Svoboda, M., Vallet, P., Wolff, B., Pretzsch, H., 2020. Species mixing reduces drought susceptibility of Scots pine (*Pinus sylvestris* L.) and oak (*Quercus robur* L., *Quercus petraea* (Matt.) Liebl.) – site water supply and fertility modify the mixing effect. For. Ecol. Manag. 461, 117908. https://doi.org/10.1016/j.foreco.2020.117908.
Szymański, S., 2001. Ekologiczne Podstawy Hodowli Lasu. PWRiL, Warszawa.
Thurm, E.A., Pretzsch, H., 2016. Improved productivity and modified tree morphology of mixed versus pure stands of European beech (*Fagus sylvatica*) and Douglas-fir (*Pseudotsuga menziesii*) with increasing precipitation and age. Ann. For. Sci. 73, 1047–1061. https://doi.org/10.1007/s13595-016-0588-8.
Topcuoglu, A., 1940. Die Verteilung des Zuwachses auf die Schaftlänge der Bäume. In: Tharandter Forstliches Jahrbuch, vol. 91. Paul Parey, Berlin, pp. 485–554.
Turner, D.P., Koerper, G.J., Harmon, M.M., Jeffrey, J.L., 1995. A carbon budget for forests of the conterminous United States. Ecol. Appl. 5, 421–463.
Vannoppen, A., Kint, V., Ponette, Q., Verheyen, K., Muys, B., 2019. Tree species diversity impacts average radial growth of beech and oak trees in Belgium, not their long-term growth trend. For. Ecosyst. 6, 10. https://doi.org/10.1186/s40663-019-0169-z.
Vítková, M., Müllerová, J., Sádlo, J., Pergl, J., Pyšek, P., 2017. Black locust (*Robinia pseudoacacia*) beloved and despised: a story of an invasive tree in Central Europe. For. Ecol. Manag. 384, 287–302. https://doi.org/10.1016/j.foreco.2016.10.057.
Vospernik, S., Heym, M., Pretzsch, H., Pach, M., Steckel, M., Aldea, J., Brazaitis, G., Bravo-Oviedo, A., Del Rio, M., Löf, M., Pardos, M., Bielak, K., Bravo, F., Coll, L., Černý, J., Droessler, L., Ehbrecht, M., Jansons, A., Korboulewsky, N., Jourdan, M., Nord-Larsen, T., Nothdurft, A., Ruiz-Peinado, R., Ponette, Q., Sitko, R., Svoboda, M., Wolff, B., 2023. Tree species growth response to climate in mixtures of *Quercus robur*/*Quercus petraea* and *Pinus sylvestris* across Europe – a dynamic, sensitive equilibrium. For. Ecol. Manag. 530, 120753. https://doi.org/10.1016/j.foreco.2022.120753.
Wagner, R.G., Radosevich, S.R., 1998. Neighborhood approach for quantifying interspecific competition in coastal Oregon forests. Ecol. Appl. 8, 779–794. https://doi.org/10.1890/1051-0761(1998)008[0779:NAFQIC]2.0.CO;2.
Warner, E., Cook-Patton, S.C., Lewis, O.T., Brown, N., Koricheva, J., Eisenhauer, N., Ferlian, O., Gravel, D., Hall, J.S., Jactel, H., Mayoral, C., Meredieu, C., Messier, C., Paquette, A., Parker, W.C., Potvin, C., Reich, P.B., Hector, A., 2023. Young mixed planted forests store more carbon than monocultures—a meta-analysis. Front. For. Glob. Change 6, 1226514. https://doi.org/10.3389/ffgc.2023.1226514.
Wiatrowska, B., Kurek, P., Moroń, D., Celary, W., Chrzanowski, A., Trzciński, P., Piechnik, Ł., 2023. Linear scaling – negative effects of invasive *Spiraea tomentosa* (Rosaceae) on wetland plants and pollinator communities. NeoBiota 81, 63–90. https://doi.org/10.3897/neobiota.81.95849.
Wickham, H., 2016. ggplot2: Elegant Graphics for Data Analysis. Springer-Verlag, New York.
Wohlgemuth, T., Gossner, M.M., Campagnaro, T., Marchante, H., van Loo, M., Vacchiano, G., Castro-Díez, P., Dobrowolska, D., Gazda, A., Keren, S., Keserű, Z., Koprowski, M., La Porta, N., Marozas, V., Nygaard, P.H., Podrázský, V., Puchałka, R., Reisman-Berman, O., Straigytė, L., Ylioja, T., Pötzelsberger, E., Silva, J.S., 2022. Impact of non-native tree species in Europe on soil properties and biodiversity: a review. NeoBiota 78, 45–69. https://doi.org/10.3897/neobiota.78.87022.
Woziwoda, B., Dyderski, M.K., Jagodziński, A.M., 2021. Forest land use discontinuity and northern red oak *Quercus rubra* introduction change biomass allocation and life strategy of lingonberry *Vaccinium vitis-idaea*. For. Ecosyst. 8, 9. https://doi.org/10.1186/s40663-021-00287-y.
Yang, K., Zhu, J., Zhang, W., Gu, J., Wang, Z., Xu, S., 2022. Comparison of soil chemical and microbial properties in monoculture larch and mixed plantations in a temperate forest ecosystem in Northeast China. Ecol. Process. 11, 12. https://doi.org/10.1186/s13717-022-00358-0.
Zasada, M., 2017. Raport Końcowy Z Tematu Badawczego "Ekologiczne, Gospodarcze I Urządzeniowe Konsekwencje Występowania Wybranych Gatunków Drzew Obcych W Polsce" Realizowanego W Latach 2013-2017 Przez Samodzielną Pracownię Dendrometrii I Nauki O Produkcyjności Lasu Na Zlecenie Dyrekcji Generalnej Lasów Państwowych W Warszawie. SGGW, Warszawa.

Table S1. List of all woody species present in study plots and allometric models used for foliage biomass estimation (**Table S2**).

Species	**Taxa group**
Acer campestre L.	*Acer*
Acer negundo L.	*Acer*
Acer platanoides L.	*Acer*
Acer pseudoplatanus L.	*Acer*
Amelanchier spicata K.Koch	*Amelanchier*
Aronia melanocarpa (Michx.) Elliott	*Cornus*
Betula pendula Roth	*Betula*
Betula pubescens Ehrh.	*Betula*
Carpinus betulus L.	*Carpinus*
Carya ovata (Mill.) K.Koch	Broadleaved
Prunus avium (L.) L.	*Prunus*
Cornus sanguinea L.	*Cornus*
Corylus avellana L.	*Corylus*
Crataegus laevigata DC.	*Prunus serotina*
Crataegus monogyna Jacq.	*Prunus serotina*
Crataegus rhipidophylla Gand.	*Prunus serotina*
Euonymus europaeus L.	*Cornus*
Fagus sylvatica L.	*Fagus*
Frangula alnus Mill.	*Frangula*
Fraxinus excelsior L.	*Fraxinus*
Larix decidua Mill.	*Larix*
Picea abies (L.) H.Karst.	*Picea*
Pinus sylvestris L.	*Pinus*
Prunus domestica L.	*Prunus serotina*
Prunus padus L.	*Prunus serotina*
Prunus serotina Ehrh.	*Prunus serotina*
Pseudotsuga menziesii (Mirb.)	*Picea*
Quercus petraea (Matt.) Liebl.	*Quercus*
Quercus robur L.	*Quercus*
Quercus rubra L.	*Quercus*
Rhamnus cathartica L.	*Cornus*
Ribes spicatum Robson	*Ribes*
Ribes uva-crispa L.	*Ribes*
Robinia pseudoacacia L.	*Robinia*
Sambucus nigra L.	*Sambucus*
Sambucus racemosa L.	*Sambucus*
Sorbus aucuparia L.	*Sorbus*
Tilia cordata Mill.	Broadleaved
Tilia platyphyllos Scop.	Broadleaved
Ulmus laevis Pall.	*Ulmus*
Ulmus minor Mill.	*Ulmus*

Table S2. Allometric equations determining foliage biomass of particular tree species recorded on the study plots. Equations adopted were established for habitat conditions similar to those of this study. Abbreviations: DBH – diameter at breast height; CF - correction factor to reverse transformation of log-log models. Biomass components: AB – total aboveground biomass, ABW – aboveground woody biomass, FL – foliage biomass. Taxa group is referenced to particular species in **Table S1**.

Taxa group	Biomass component	Unit	Source	R^2	*N*	DBH min (cm)	DBH max (cm)	Formula	*a*	*b*	CF
Acer	ABW	kg	Forrester et al. 2017	0.941	231	0	25	$\ln(Y)=\ln(a)+b\times\ln(D)$, CF	–2.31160	2.41860	1.01050
Acer	ABW	kg	Forrester et al. 2017	0.969	3521	25	88	$\ln(Y)=\ln(a)+b\times\ln(D)$, CF	–2.16530	2.41430	1.04148
Acer	FL	kg	Forrester et al. 2017	0.789	70	0	88	$\ln(Y)=\ln(a)+b\times\ln(D)$, CF	–4.06250	2.06620	1.00318
Amelanchier	AB	g	Brown 1976	0.990	39	0.4	4.5	$\ln(y)=a\ b\times\ln(X)$	3.60700	2.88700	NA
Amelanchier	FL	g	Brown 1976	0.830	39	0.4	4.5	$\ln(y)=a+b\times\ln(X)$	1.69100	2.11100	NA
Betula	ABW	kg	Forrester et al. 2017	0.988	449	0	38	$\ln(Y)=\ln(a)+b\times\ln(D)$, CF	–2.21180	2.37710	1.00799
Betula	FL	kg	Forrester et al. 2017	0.903	231	0	38	$\ln(Y)=\ln(a)+b\times\ln(D)$, CF	–4.13700	1.88610	1.16321
Broadleaved	ABW	kg	Forrester et al. 2017	0.969	3521	0	88	$\ln(Y)=\ln(a)+b\times\ln(D)$, CF	–2.16530	2.41430	1.04148
Broadleaved	FL	kg	Forrester et al. 2017	0.847	1824	0	88	$\ln(Y)=\ln(a)+b\times\ln(D)$, CF	–4.22860	1.86250	1.06365
Carpinus betulus	AB	kg	Jagodziński, unpbl.	0.965	38	0	20	$Y=a\times D\text{^}b$	0.04670	2.67655	NA
Carpinus betulus	FL	kg	Jagodziński, unpbl.	0.875	38	0	20	$Y=a\times D\text{^}b$	0.01996	1.95261	NA
Cornus sanguinea	AB	kg	Jagodziński, unpbl.	0.892	52	0	8	$Y=a\times D\text{^}b$	1.29073	1.23701	NA
Cornus sanguinea	FL	kg	Jagodziński, unpbl.	0.734	52	0	8	$Y=a\times D\text{^}b$	0.13820	1.12562	NA
Corylus avellana	AB	kg	Jagodziński, unpbl.	0.926	96	0	16	$Y=a\times D\text{^}b$	0.65347	1.37869	NA
Corylus avellana	FL	kg	Jagodziński, unpbl.	0.668	96	0	16	$Y=a\times D\text{^}b$	0.09715	0.92685	NA
Fagus	ABW	kg	Forrester et al. 2017	0.975	712	0	82	$\ln(Y)=\ln(a)+b\times\ln(D)$, CF	–1.78430	2.38950	1.09215
Fagus	FL	kg	Forrester et al. 2017	0.883	330	0	73	$\ln(Y)=\ln(a)+b\times\ln(D)$, CF	–4.48130	1.90730	1.08752
Frangula alnus	AB	kg	Jagodziński, unpbl.	0.852	74	0	87	$Y=a\times D\text{^}b$	0.16494	1.72121	NA
Frangula alnus	FL	kg	Jagodziński, unpbl.	0.704	74	0	87	$Y=a\times D\text{^}b$	0.03785	0.94933	NA
Fraxinus	ABW	kg	Forrester et al. 2017	0.946	330	0	40	$\ln(Y)=\ln(a)+b\times\ln(D)$, CF	–2.54360	2.61840	0.94631
Fraxinus	FL	kg	Forrester et al. 2017	0.872	158	0	69	$\ln(Y)=\ln(a)+b\times\ln(D)$, CF	–4.85020	2.40640	0.80923
Larix	AB	kg	Jagodziński et al. 2018	0.971	96	2	58	$Y=a\times D\text{^}b$	0.13800	2.39070	NA
Larix	FL	kg	Jagodziński et al. 2018	0.767	96	2	58	$Y=a\times D\text{^}b$	0.00460	2.10360	NA
Picea	ABW	kg	Forrester et al. 2017	0.970	668	0	77	$\ln(Y)=\ln(a)+b\times\ln(D)$, CF	–2.04640	2.30480	1.03300

Picea	FL	kg	Forrester et al. 2017	0.906	1007	0	77	ln(*Y*)=ln(a)+*b*×ln(*D*), CF	–2.79570	1.86880	1.02003
Pinus	AB	kg	Jagodziński et al. 2019	0.976	549	0	65	*Y*=*a*×*D*^*b*	0.20760	2.21850	NA
Pinus	FL	kg	Jagodziński et al. 2019	0.841	549	0	65	*Y*=*a*×*D*^*b*	0.03020	1.74200	NA
Prunus	ABW	kg	Forrester et al. 2017	0.987	99	0	50	ln(*Y*)=ln(a)+*b*×ln(*D*), CF	–1.09680	2.09200	1.02629
Prunus	FL	kg	Forrester et al. 2017	0.545	99	0	50	ln(*Y*)=ln(a)+*b*×ln(*D*), CF	–4.10580	1.32120	0.95641
Prunus serotina	AB	kg	Jagodziński, unpbl.	0.974	50	0	15	*Y*=*a*×*D*^*b*	0.84778	1.44607	NA
Prunus serotina	FL	kg	Jagodziński, unpbl.	0.937	50	0	15	*Y*=*a*×*D*^*b*	0.04973	1.86895	NA
Quercus	ABW	kg	Forrester et al. 2017	0.990	579	0	77	ln(*Y*)=ln(a)+*b*×ln(*D*), CF	–2.31490	2.51330	1.03670
Quercus	FL	kg	Forrester et al. 2017	0.911	99	0	68	ln(*Y*)=ln(a)+*b*×ln(*D*), CF	–4.46630	2.13750	0.96633
Ribes	AB	g	Brown 1976	0.900	37	0.4	1.4	ln(*y*)=*a*+ *b*×ln(*X*)	3.89200	3.12200	NA
Ribes	FL	g	Brown 1976	0.630	37	0.4	1.4	ln(*y*)=*a*+ *b*×ln(*X*)	2.16400	2.53800	NA
Robinia	AB	kg	Zasada 2017	NA	22	7	46	*Y*=*a*×*D*^*b*	0.00030	2.51800	NA
Robinia	ABW	kg	Forrester et al. 2017	0.923	165	0	24	ln(*Y*)=ln(*a*)+*b*×ln(*D*), CF	–2.53440	2.45980	1.02110
Robinia	FL	kg	Forrester et al. 2017	0.936	99	0	24	ln(*Y*)=ln(*a*)+*b*×ln(*D*), CF	–2.79850	1.12780	1.02069
Robinia	FL	kg	Zasada 2017	NA	22	7	46	*Y*=*a*×*D*^*b*	0.00150	1.52880	NA
Sambucus nigra	AB	kg	Jagodziński, unpbl.	0.634	60	0	10	*Y*=*a*×*D*^*b*	1.34743	1.06650	NA
Sambucus nigra	FL	kg	Jagodziński, unpbl.	0.479	60	0	10	*Y*=*a*×*D*^*b*	0.18051	0.79876	NA
Sorbus aucuparia	AB	kg	Jagodziński, unpbl.	0.929	64	0	9	*Y*=*a*×*D*^*b*	0.15992	2.16383	NA
Sorbus aucuparia	FL	kg	Jagodziński, unpbl.	0.792	64	0	9	*Y*=*a*×*D*^*b*	0.02302	1.66533	NA
Ulmus	ABW	kg	Forrester et al. 2017	0.847	1824	0	88	ln(*Y*)=ln(*a*)+*b*×ln(*D*), CF	–4.22860	1.86250	1.06365
Ulmus	ABW	kg	Alberti et al. 2005	0.970	10	0	31	*Y*=*a*×*D*^*b*	0.10000	2.56000	NA
Ulmus	FL	kg	Forrester et al. 2017	0.969	3521	0	88	ln(*Y*)=ln(*a*)+*b*×ln(*D*), CF	–2.16530	2.41430	1.04148
Ulmus	FL	kg	Alberti et al. 2005	0.980	10	0	31	*Y*=*a*×*D*^*b*	0.13000	1.12000	NA

Table S3. Generalized Linear Mixed-Effects models (Beta distribution) for relative aboveground biomass (AB) increment As a function of of absolute biomass of *R. pseudoacacia* and *P. serotina* (Inv. biomass), diameter at breast height (DBH, at tree level) or stand age (at stand level), and their intercation

	Robinia pseudoacacia						*Prunus serotina*				
	Variable	**Estimate**	**SE**	***z***	***p***		**Variable**	**Estimate**	**SE**	***z***	***p***
Tree level:						**Tree level:**					
Oak	(Intercept)	–9.850e-01	2.078e-01	–4.741	2.13e-06	**Oak**	(Intercept)	–1.153827	0.192042	–6.008	1.88e-09
plots= 24	DBH	–1.713e-02	4.539e-03	–3.774	0.000161	plots= 24	DBH	–0.010253	0.004480	–2.288	0.0221
obs.= 118	Inv. biomass	–4.882e-03	2.265e-03	–2.155	0.031124	obs.= 119	Inv. biomass	0.030047	0.037701	0.797	0.4255
$AICc_0$= –362.9	DBH×Inv. biomass	8.569e-05	4.344e-05	1.973	0.048548	$AICc_0$= –373.6	DBH×Inv. biomass	–0.001169	0.001286	–0.908	0.3636
AICc= –362.2						AICc= –375.8					
σ^2= 0.0682						σ^2= 0.0347					
σ= 0.2611						σ= 0.1863					
Pine	(Intercept)	–1.956e+00	4.471e-01	–4.375	1.21e-05	**Pine**	(Intercept)	–0.925866	0.488248	–1.896	0.0579
plots= 24	DBH	9.027e-03	1.444e-02	0.625	0.532	plots= 24	DBH	–0.021061	0.016287	–1.293	0.1960
obs.= 117	Inv. biomass	2.882e-03	9.648e-03	0.299	0.765	obs.= 119	Inv. biomass	–0.055742	0.070097	–0.795	0.4265
$AICc_0$= –318.1	DBH×Inv. biomass	–9.898e-05	3.126e-04	–0.317	0.752	$AICc_0$= –375.8	DBH×Inv. biomass	0.002425	0.002100	1.155	0.2482
AICc= –323.5						AICc= –373.0					
σ^2= 0.2777						σ^2= 0.0345					
σ= 0.572						σ= 0.1856					
Stand level:						**Stand level:**					
Oak	(Intercept)	–2.798e-01	5.457e-02	–5.129	2.92e-07	**Oak**	(Intercept)	–2.512e-01	4.988e-02	–5.036	4.74e-07
obs.= 24	Stand age	–7.946e-04	5.612e-04	–1.416	0.157	obs.= 24	Stand age	–7.816e-04	5.350e-04	–1.461	0.144
$AICc_0$= –119.3	Inv. biomass	–4.348e-04	7.287e-04	–0.597	0.551	$AICc_0$= –119.0	Inv. biomass	2.812e-03	9.569e-03	0.294	0.769
AICc= –121.7	Stand age×Inv.biomass	5.083e-06	8.605e-06	0.591	0.555	AICc= –121.7	Stand age×Inv.biomass	–9.005e-05	1.649e-04	–0.546	0.585
Pine						**Pine**					
obs.= 24	(Intercept)	–0.4113092	0.2683490	–1.533	0.125	obs.= 24	(Intercept)	–0.3382644	0.3425189	–0.988	0.323359
$AICc_0$= –60.2	Stand age	–0.0150827	0.0036929	–4.084	4.42e-05	$AICc_0$= –54.5	Stand age	–0.0160311	0.0045707	–3.507	0.000453
AICc= –60.4	Inv. biomass	0.0122409	0.0123819	0.989	0.323	AICc= –60.2	Inv. biomass	–0.0173712	0.0831533	–0.209	0.834522
	Stand age×Inv.biomass	–0.0002397	0.0002171	–1.104	0.269		Stand age×Inv.biomass	0.0004681	0.0010208	0.459	0.646561

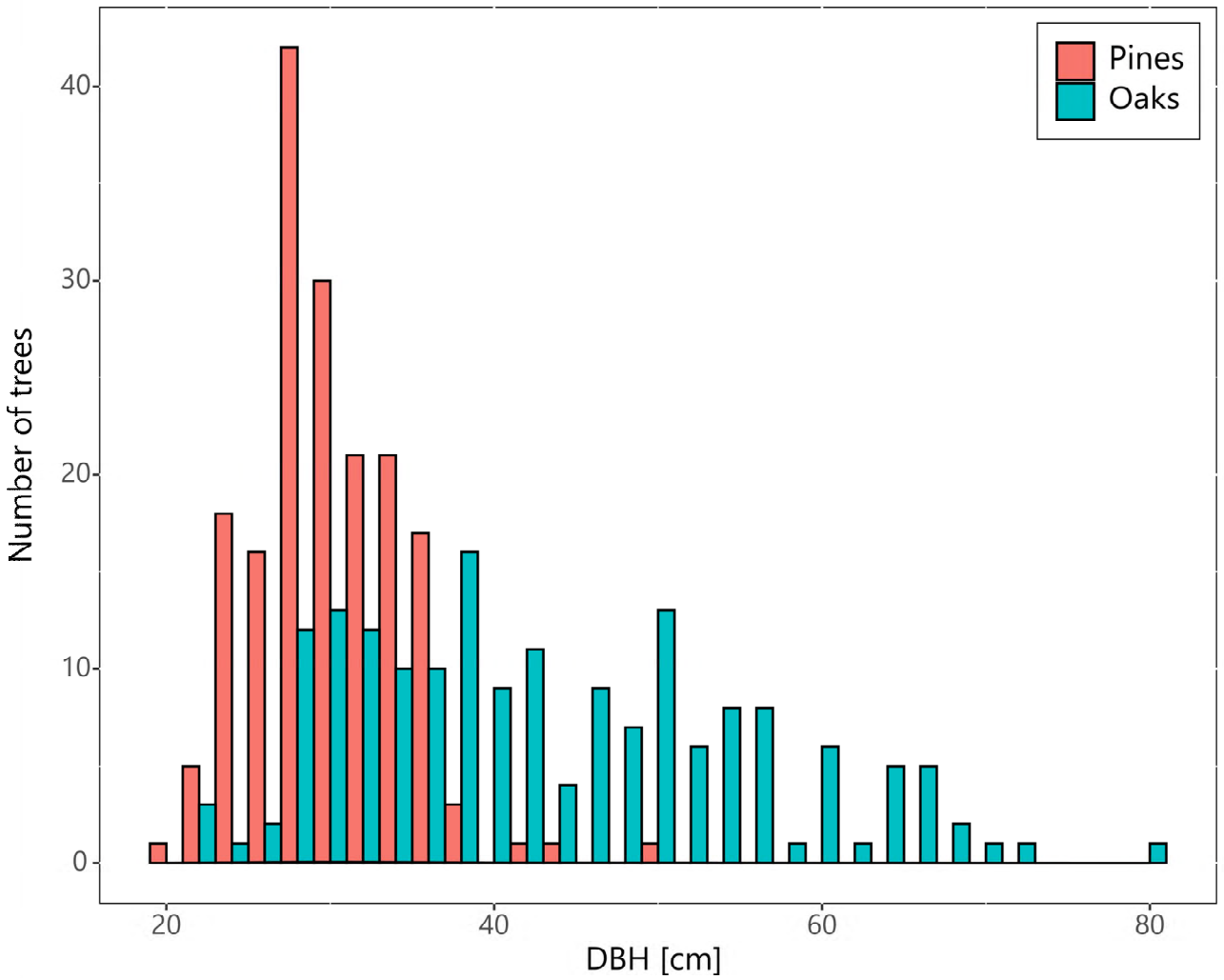

Fig.S1 Distributions of sampled trees diameter at breast high (DBH)

References

Alberti, G., Candido, P., Peressotti, A., Turco, S., Piussi, P., Zerbi, G., 2005. Aboveground biomass relationships for mixed ash (*Fraxinus excelsior* L. and *Ulmus glabra* Hudson) stands in Eastern Prealps of Friuli Venezia Giulia (Italy). Ann. For. Sci. 62, 831–836. https://doi.org/10.1051/forest:2005089

Brown, J.K., 1976. Estimating shrub biomass from basal stem diameters. Can. J. For. Res. 6, 153–158. https://doi.org/10.1139/x76-019

Forrester, D.I., Tachauer, I.H.H., Annighoefer, P., Barbeito, I., Pretzsch, H., Ruiz-Peinado, R., Stark, H., Vacchiano, G., Zlatanov, T., Chakraborty, T., Saha, S., Sileshi, G.W., 2017. Generalized biomass and leaf area allometric equations for European tree species incorporating stand structure, tree age and climate. For. Ecol. Manag. 396, 160–175. https://doi.org/10.1016/j.foreco.2017.04.011

Jagodziński, A.M., Dyderski, M.K., Gęsikiewicz, K., Horodecki, P., 2019. Effects of stand features on aboveground biomass and biomass conversion and expansion factors based on a *Pinus sylvestris* L. chronosequence in Western Poland. Eur. J. For. Res. 138, 673–683. https://doi.org/10.1007/s10342-019-01197-z

Jagodziński, A.M., Dyderski, M.K., Gęsikiewicz, K., Horodecki, P., 2018. Tree- and Stand-Level Biomass Estimation in a *Larix decidua* Mill. Chronosequence. Forests 9, 587. https://doi.org/10.3390/f9100587

Zasada, M., 2017. Raport końcowy z tematu badawczego "Ekologiczne, gospodarcze i urządzeniowe konsekwencje występowania wybranych gatunków drzew obcych w Polsce" realizowanego w latach 2013-2017 przez Samodzielną Pracownię Dendrometrii i Nauki o Produkcyjności Lasu na zlecenie Dyrekcji Generalnej Lasów Państwowych w Warszawie. SGGW, Warszawa.

Publikacja 2.

Sebastian Bury, Marcin K. Dyderski

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Research Article

Invasive *Prunus serotina* vs. *Robinia pseudoacacia*: How does temperate forest natural regeneration respond to their quantity?

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Abstract

Invasive trees negatively impact forests, by making the vegetation more homogeneous when invaders are present than when they are absent. Here, we aim to more deeply understand the effects of invasive trees on forests with a focus on seedlings and saplings and how they respond to continuous variation in aboveground biomass of invaders rather than presence/absence. Our findings are useful for close-to-nature silviculture, as they elucidate how much natural regeneration will change under particular biomasses of invasive species. Specifically, we evaluate the relationships of two invasive tree species: black cherry *Prunus serotina* Ehrh. and black locust *Robinia pseudoacacia* L. with natural tree regeneration in temperate forests. We established 160 circular 0.05 ha plots in western Poland managed forests, in two different habitat types: nutrient-poor with *Pinus sylvestris* L. and nutrient-rich with *Quercus* spp. We assessed natural regeneration by counting all trees < 1.3 m in height, within four circular subplots (r = 3 m). Relationships between invader biomass and regeneration of other tree species were idiosyncratic. Natural regeneration of dominant forest-forming tree species (*P. sylvestris*, *Quercus petraea*) decreased with increasing invader biomass, while shade-tolerant, nitrophilous tree and shrub regeneration increased with invader biomass. The most negatively correlated were *P. sylvestris* in nutrient-poor habitats and *Q. petraea* in both nutrient-poor and rich habitats. We observed increased density of other non-native species as *R. pseudoacacia* abundance increased, in line with the invasional meltdown hypothesis.

Key words: Advance regeneration, black cherry, black locust, invader aboveground biomass, invasion ecology, *per capita* effect, saplings, seedlings

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Introduction

Regeneration is a crucial element of forest stability and continuity (Oliver and Larson 1996; Baraloto et al. 2005; Käber et al. 2023). This process occurs through planting or sowing — artificial regeneration, or naturally without human impact — natural regeneration (Jaworski et al. 2007; Nyland 2007). Natural regeneration is essential in natural forests, without human impact, but also plays an increasing role in managed forests. Using natural regeneration of forests is part of what is called close-to-nature, ecological forestry (Batavia and Nelson 2016; Palik and D'Amato 2017). Closer to nature forestry is based to a greater extent on the natural dynamics of tree stands, which results in an increase in the complexity of their structure and increased biodiversity (European Commission 2023). Naturally regenerated stands are characterized by higher genetic diversity than forest

plantations. Such stands are therefore characterized by greater resistance and greater adaptation to local environmental conditions (Jaworski et al. 2007; European Commission 2023). Additionally, natural regeneration is more cost-effective than artificial regeneration (Oluwajuwon et al. 2024).

The natural regeneration of forests is shaped by abiotic and biotic factors. Abiotic factors include climate (Canham and Murphy 2017), light availability (Minotta and Pinzauti 1996; Modrý et al. 2004), and soil characteristics (Minotta and Pinzauti 1996; Madsen and Larsen 1997; Modrý et al. 2004). Biotic factors include diseases (e.g., Bakys et al. 2009; Lygis et al. 2014; Turczański et al. 2021), herbivory (Ammer 1996; Bruinderink and Hazebroek 1996; Iszkuło et al. 2013; Borkowski et al. 2017; Szwagrzyk et al. 2020) and competition with other plants (Mölder et al. 2019; deGroot et al. 2022; Li et al. 2023). Disturbances, including fire (Il'ichev et al. 2011) and windthrows (Szwagrzyk et al. 2018) can create gaps in the forest that alter both the abiotic and biotic environment and provide good conditions for the growth of young trees. Additionally, natural regeneration relies on seed availability (Howe and Smallwood 1982; Bartlow et al. 2018; Czortek et al. 2024). Finally, natural regeneration processes are influenced by human activities related to forest management, e.g., timber harvesting (Tavankar et al. 2017; Picchio et al. 2020), post-disturbance management (Marcolin et al. 2019), and climate change (Boucher et al. 2020; Enríquez-de-Salamanca 2022). Thus, natural regeneration depends on many factors, abiotic and biotic, natural and influenced by humans. Many of these factors that influence forest regeneration can be further shaped by invasive species, which alter both the abiotic and biotic environment.

Invasive trees and shrubs are well known for their ability to transform the recipient ecosystem (e.g., Crooks 2002; Corenblit et al. 2014; Jagodziński et al. 2024), e.g., by changes in nutrient cycling and decomposition (Aerts et al. 2017; Horodecki et al. 2019) or light availability (Starfinger et al. 2003; Dyderski and Jagodziński 2019; García et al. 2023). Those transformations can also impact the understory, including saplings and seedlings (Fuentes-Ramírez et al. 2011; Terwei et al. 2013; Dyderski and Jagodziński 2020; Langmaier and Lapin 2020). A review of studies assessing the impact of invasive plants on natural regeneration (Langmaier and Lapin 2020) identified 74 studies in Europe. Most of these studies evaluate natural regeneration based on cover and have revealed important impacts of invasive species (e.g., Maskell et al. 2006; Hejda 2012; Petrášová et al. 2013; Tinya et al. 2019). Cover, though important, does not provide reliable estimates of population size, and thus additional research on the impacts of forest invaders using precise counts of seedlings and saplings will aid in projecting forest health into the future (Terwei et al. 2013). Additionally, most studies on forest invasion compared invaded stands with uninvaded ones (Gentili et al. 2019; Lanta et al. 2022; Slabejová et al. 2023). While this is an important first step, understanding the effects of invader abundance, i.e. the *per capita* effects of invasive plants will provide more actionable information for forest management. This has only rarely been done for either herbaceous plants (Czortek et al. 2023; Wiatrowska et al. 2023) or invasive woody plants (Chabrerie et al. 2008; López-Núñez et al. 2017; García et al. 2023; Bury and Dyderski 2024b, 2024a; Jagodziński et al. 2024) with a focus on biodiversity or ecosystems services. However, to our knowledge, there are no studies assessing the effects of invader abundance on native species natural regeneration.

To address these knowledge gaps, we investigated the relationship between forest natural regeneration and the abundance of two invasive tree species, *Prunus serotina*

and *Robinia pseudoacacia*. To capture various environmental contexts, we focused on two forest types dominated by either *Pinus sylvestris* or *Quercus* spp.

Prunus serotina and *Robinia pseudoacacia* differ in their biology and ecology. Both are native to North America and were introduced to Europe in the 17th century as ornamental trees. In the following centuries, they were planted by foresters as soil-improving and wood-production trees (Starfinger et al. 2003; Cierjacks et al. 2013). Currently, *P. serotina* (Starfinger et al. 2003) and *R. pseudoacacia* (Sádlo et al. 2017; Vítková et al. 2017; Slabejová et al. 2023) are common invasive trees in Central Europe. *Prunus serotina* is mostly a shrub or small tree found in gaps (Godefroid et al. 2005; Closset-Kopp et al. 2007, 2011). It is mostly dispersed by mammals (Kurek et al. 2024), birds, or gravity (Starfinger et al. 2003; Deckers et al. 2008). *Prunus serotina* increases the soil nutrient pool, compared to native tree species, due to the higher leaf nutrient content and decomposition rate (Aerts et al. 2017; Horodecki et al. 2019). *Robinia pseudoacacia* is a pioneer tree associated with big, open patches that attains large size and occurs in the highest forest strata (Cierjacks et al. 2013; Bury and Dyderski 2024b), associated with big, open patches. Seeds of *R. pseudoacacia* are dispersed by wind and gravity (Vítková et al. 2017), though much of its spread is vegetative (Bouteiller et al. 2023). As a tree in the Fabaceae, *R. pseudoacacia* creates symbiosis with nitrifying bacteria (Rice et al. 2004; Vítková et al. 2017) and thus delivers a large amount of nitrogen to the soil largely through leaf litter (Rahmonov 2009).

We address five hypotheses in our work. (H1) We hypothesized that patterns of forest regeneration will differ in association with the two invaders. We assume that *R. pseudoacacia* and *P. serotina* will shape interactions among species and their environment in different ways, which will be manifested by different patterns of natural regeneration densities (Dyderski and Jagodziński 2020; Langmaier and Lapin 2020). (H2) We expected the regeneration of trees and shrubs to vary with invader abundance in species-specific ways (Terwei et al. 2013; Dyderski and Jagodziński 2018). (H3) Likewise, we hypothesized that there would be differences between nutrient-rich and nutrient-poor sites (Chmura 2004; Halarewicz 2011). (H4) We hypothesized that other non-native tree species may have higher regeneration densities in the presence of studied invaders, according to the invasional meltdown hypothesis (Simberloff and Holle 1999). Finally, we aimed to compare patterns obtained using three different statistical approaches (ordination, Threshold Indicator Taxa Analysis, and generalized linear mixed-effects models) to provide insights into which is best suited to the type of data we collected. (H5) We hypothesized that these three methods would provide consistent results regarding the effects of studied invaders on particular tree species' natural regeneration.

Methods

Study area and study design

We conducted the study in managed forests in western Poland, in five forest districts: Babki, Czerniejewo, Jarocin, Konstantynowo, and Łopuchówko (Fig. 2). We located study plots between 51°59'4.08"N and 52°40'9.36"N and 16°35'28.98"E and 17°37'13.26"E, in two geographical regions: the Greater Poland Lakeland (northern part) and Greater Poland Lowland (southern part). The climatic conditions are similar in the study area with an annual temperature of 8.5 °C and mean annual precipitation of 500–550 mm (BDL 2024).

We aimed to sample a quantitative gradient of invader biomass. To obtain a range, we selected study plots based on invader cover, which is straightforward to estimate, and then, after plots were chosen, we quantified aboveground biomass, following established methods (Bury and Dyderski 2024b), and described in more detail below. During initial plot selection we search for control plots (zero individuals of studied invaders ≥ 1.3 m height), medium (< 30% cover), and high (> 50%) cover areas. Therefore, in our plots there could have been *P. serotina* or *R. pseudoacacia* individuals shorter than 1.3 m (included in the natural regeneration survey), however, they were rare as the density of studied neophytes depends on the proximity of propagule sources (Dyderski and Jagodziński 2018). When calculating the gradient of invader biomass, we accounted only for individuals taller than 1.3 m, and the biomass of those few individuals in the regeneration layer in control plots was negligible. We stratified our samples into two habitat types: nutrient-rich habitats that are typical of the invasive species in their native range, and nutrient-poor, where invaders had been massively introduced to improve these habitats (Starfinger et al. 2003; Cierjacks et al. 2013). Nutrient-poor sites included *Leucobryo-Pinetum* W. Mat. (1962) 1973 communities or secondary *P. sylvestris* forests. In our study, nutrient-rich sites include different subtypes of *Galio sylvatici-Carpinetum betuli* Oberd. 1957 communities or secondary *Quercus* spp. forests. Some areas had characteristics of poorer communities or slightly more fertile ones, with species characteristic of *Potentillo albae-Quercetum* Libb. 1933 or *Querco-roboris Pinetum* Mat. et Polak. 1955 s.l. We also included two management contexts: stands in the middle of rotation age (medium age) and close to rotation age (mature age), as these age classes differ in light conditions beneath stand canopies. Stands in the middle age and those of close to rotation age differ in structure and growth dynamics (Jiang et al. 2017; Li et al. 2024). Middle-aged stands are characterized by a rapid increase in biomass, while stands close to rotation age are characterized by maximum biomass, but its increment decreases with age (Jiang et al. 2017; Li et al. 2024). Stand age is related to light availability by stem density and canopy closure, as well as in terms of higher species richness of forest specialists, related to a longer time since disturbance (Jagodziński and Oleksyn 2009; Felton et al. 2010; Conradi et al. 2020). In total, we established 160 plots (500 m^2 per plot), including 32 control plots (8 replications × 2 habitat types × 2 stand age classes), 64 plots with *R. pseudoacacia* (8 replications × 2 invasion levels × 2 habitat types × 2 stand age classes) and 64 plots with *P. serotina* (same as *R. pseudoacacia*) (Fig. 1). Plots representing the same plot variant (invader × invasion level × habitat × stand age) were a minimum of 5 km apart to reduce spatial autocorrelation.

Invasive species quantitative gradient — aboveground biomass

We estimated invader biomass of 102 plots in the autumn of 2021 and 2022, measuring the diameter at breast height (DBH) of all the individuals in the plots following García et al. (2023). The other 58 plots were sampled in autumn 2022 and 2023. For these, we measured the diameter at the breast height only on trees larger than 5 cm, and we counted trees thinner than 5 cm by species. Then, from the database of the 102 plots, we calculated the average DBH of individuals thinner than 5 cm by species (Suppl. material 1: table S1 for mean and SD values). This approach should not affect the validity of the

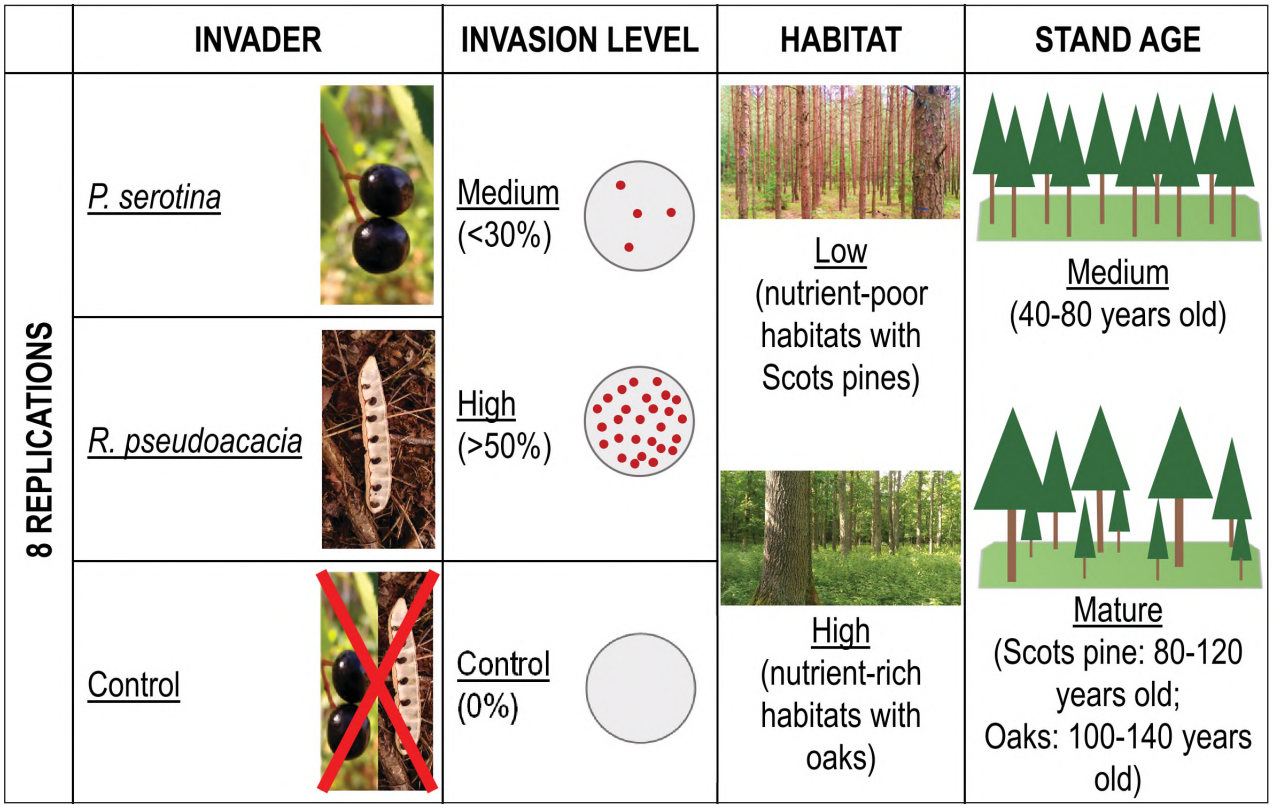

Figure 1. Scheme of the study design. Photos: S. Bury.

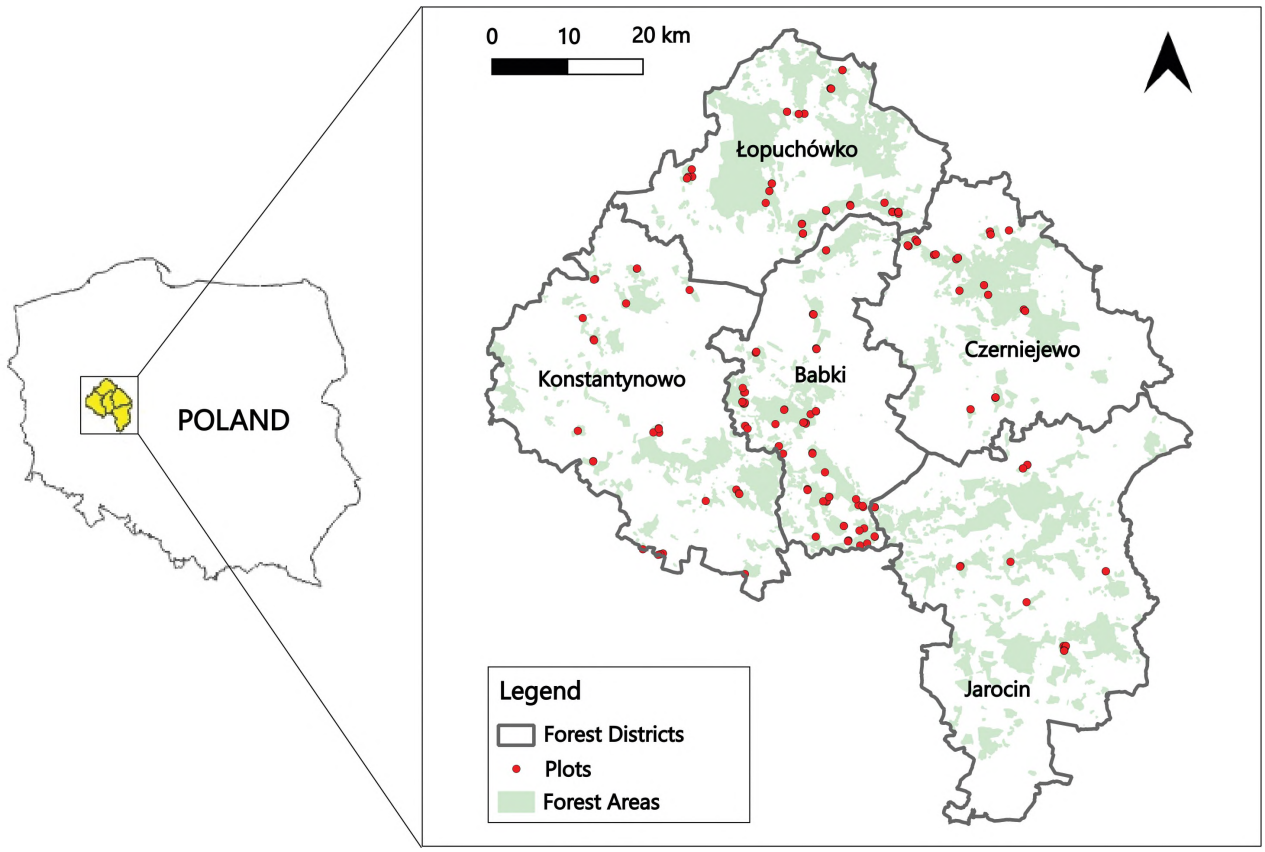

Figure 2. Distribution of the study plots (n = 160). The background map of forest cover comes from the Forest Data Bank (BDL 2024).

results, and indeed is more detailed than previous studies that either omitted trees with DBH < 5 cm or used a DBH midpoint for smaller trees (Dyderski and Jagodziński 2021a). Then, we used published allometric formulas (Suppl. material 1: tables S2–S3) to calculate the aboveground biomass for individual trees and stands (Brown 1976; Alberti et al. 2005; Forrester et al. 2017; Zasada 2017; Jagodziński et al. 2018, 2019).

Assessment of natural regeneration

In the summers of 2021, 2022, and 2023 we counted natural regeneration on four schematically distributed subplots with a 3 m radius (4 × 28.26 m^2 = 113.04 m^2). The centers of the subplots were systematically set at 4.21 m (1/3 of the main plot radius) from the center of the plots in the four cardinal directions (N, E, S, W), using a compass and measuring tape (Fig. 3). Within these subplots we identified and counted all individuals of trees and shrubs < 1.3 m height, similarly to Kerr and Mackintosh (2012) and Mousavi et al. (2012). For each plot, we identified all seedlings germinated in the study year by species, as well as all saplings up to 1.3 m in height. Saplings may have been the product of prior years' seedlings, or clonal propagation. We treated all saplings growing separately from the soil as single individuals (Radtke et al. 2013).

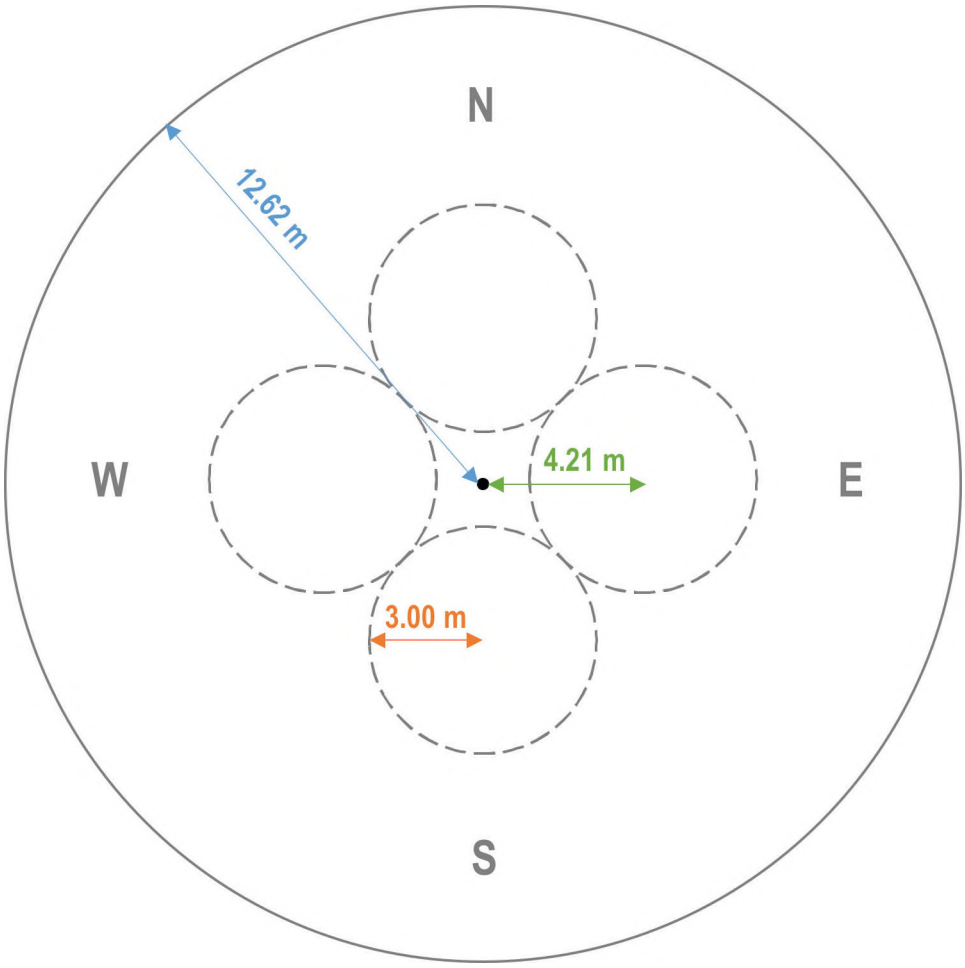

Figure 3. Schematic of the distribution of the subplots (four dashed line circles, counts of natural regeneration) within each plot (solid line circle, stand structure measurements). Plot area = 500 m^2 (r = 12.62 m), subplots area = 4 subplots × 28.26 m^2 = 113.04 m^2 (r = 3 m).

Data analyses

All analyses were conducted in R (R Core Team 2023). Because one of the plots with *P. serotina* in the stand (*P. serotina* aboveground biomass = 47.11 Mg ha^{-1}; Table 1) gave a strongly biased result, we excluded it from all analyses. The aboveground biomass of *P. serotina* trees in this area was about three times higher than the next highest result. Due to differences in species pools in each habitat type, we separately analyzed the relationships with the natural regeneration for both studied invaders on both habitats. We accounted for different stand development phases, including stand age as a covariate in analyses.

We used Canonical Correspondence Analysis (CCA) to compare the effect of invader biomass and stand age. We used the cca() function from the vegan package (Oksanen et al. 2018) to develop CCA. Due to differences in sapling density among species and plots, we log-transformed data using the decostand() function from the vegan package (Oksanen et al. 2018). Furthermore, we added invader aboveground biomass and stand age as constraints. We used the step.cca() function from the vegan package to choose the optimal set of predictors based on Akaike's Information Criterion. To assess the significance of constraints, we ran a permutation-based ANOVA-like test, implemented in the anova.cca() function. We visualized the results using the ggplot2 (Wickham 2016) and ggrepel (Slowikowski 2024) packages.

Furthermore, we used Threshold Indicator Taxa Analysis, implemented in the TITAN2 package (Baker et al. 2023) to check which sapling species increase or decrease with invader biomass. We log-transformed biomass using log(x+1) transformation, to include also plots with zero invader biomass. For species with purity and reliability ≥ 0.95 we visualized results using the plot_taxa_ridges() function with default settings. We conducted the analysis using only species that occurred in at least three plots. We did not use any additional filters in the settings. The plot_taxa_ridges() function generates graphs on which the x-axis represents an environmental factor. In our case, this is the aboveground biomass of an invasive species (log(x+1) transformation was used). Changes in the abundance of individual taxa were assessed along the gradient of the environmental variable. In our case, this was the number of saplings of individual species on the plot. Ridges are generated for species that have achieved purity and reliability of 95%. These ridges look different for each species. The shape of the ridge tells us where in the environmental gradient a given species achieves the highest probability of occurrence.

Table 1. General characteristics of the studied plots: stand age, total aboveground biomass, invasive tree species aboveground biomass. *Quercus* — nutrient-rich habitats with *Q. petraea/robur*, *Pinus* — nutrient-poor habitats with *P. sylvestris*.

	Stand age [years]				Total Aboveground Biomass [Mg ha^{-1}]				Invader Aboveground Biomass [Mg ha^{-1}]			
	Min.	**Mean**	**SD**	**Max.**	**Min.**	**Mean**	**SD**	**Max.**	**Min.**	**Mean**	**SD**	**Max.**
Control												
Quercus	47	93.75	33.28	139	157.38	278.74	100.16	507.92	0.00	0.00	0.00	0.00
Pinus	50	76.00	22.82	117	142.95	187.17	34.50	254.63	0.00	0.00	0.00	0.00
Prunus serotina												
Quercus	44	90.31	31.96	137	138.12	267.52	93.24	505.01	0.19	6.68	7.24	27.39
Pinus	45	71.59	21.78	108	142.37	196.99	33.25	256.66	0.18	7.34	8.75	47.11
Robinia pseudoacacia												
Quercus	42	94.56	34.24	139	147.63	317.01	141.48	709.91	0.82	50.77	70.37	278.24
Pinus	42	76.81	23.06	117	125.32	182.14	31.44	246.52	0.22	20.91	31.69	153.00

The top of the ridge indicates the value of the environmental indicator for which the abundance of the species is the highest. The greater the width of the ridge, the greater the discrepancies in the data. Taxa are divided into two groups. Species whose abundance increases along the environmental gradient are marked in red (increasers), while species whose abundance decreases along the environmental gradient are marked in gray/blue (they are called decliners). The z-score value indicates the strength of the impact of a given factor or, in other words, the higher the z-score, the higher the indicator value of a given species. The higher the z-score, the darker the red or gray color (for low values it is light blue). The function also generates black vertical lines on the graph. These are the so-called threshold values, which tell us where on the gradient there is a sharp change (an increase in increasers or a decrease in decliners) in the abundance of a given species.

Finally, we used Generalized Linear Mixed-Effect Models (GLMMs), using the glmmTMB package (Brooks et al. 2017), with Poisson or negative binomial family distribution, to exactly determine the relationships between the abundance of seedlings and saplings of each species with invader aboveground biomass. To test the invasional meltdown hypothesis, we also evaluated the relationships between the abundance of saplings of invasive species (excluding the dominant invader whose effects we were exploring) and invader aboveground biomass. For saplings we created models for species that occurred in at least 20% of the plots in a given variant (invader and habitat type) (Suppl. material 1: table S4). For seedlings we developed models for species that occurred in at least 10% of the plots in a given variant (invader and habitat type) (Suppl. material 1: table S13). In the Results section we present only statistically significant results (with $p < 0.05$). We used the DHARMa package (Hartig 2022) to conduct formal zero inflation and dispersion tests for each model. We started from models assuming Poisson distributions, due to the count character of our data. If we did not find problems with overdispersion we tested zero inflation, and in the case of statistically significant zero inflation, we used zero-inflated Poisson distribution. If we found statistically significant overdispersion we used negative binomial distribution, adding zero-inflation when necessary. We used invader aboveground biomass and stand age as fixed continuous effects and forest district and the year of natural regeneration assessment as random intercept, to cover spatial and temporal dependence within our dataset. We used the dredge() function of the MuMIn package (Bartoń 2017) to choose the best model according to comparing Akaike's Information Criterion of null model $AICc_0$ with the final model AICc. We presented the results using marginal responses implemented in the ggpredict() function from the ggeffects package (Lüdecke 2018). These responses show mean model prediction for each level of predictor, assuming remaining predictors at a constant (mean) level, and excluding random effects (prediction for global population). We excluded two outlying observations in the model of *Cerasus avium* saplings density for *R. pseudoacacia* in rich sites (densities: 304 and 37 ind.) and one in the model of *Carpinus betulus* saplings density for *P. serotina* rich sites (density: 1206 ind.). In these plots very high regeneration density resulted from an abundance of propagule pressure in proximity and did not allow for developing models reflecting overall conditions. We used the ggplot2 package (Wickham 2016) to present results on the graphs. In the results, we provide extreme values of sapling density for some species, i.e. zero and a value close to the maximum of the gradient for *R. pseudoacacia* and *P. serotina* in individual habitats. All mean values are followed by ± SD, except ± SE in the results of GLMMs.

Results

Within 160 plots, we recorded 56 woody plant species in the saplings, including 12 alien species. For seedlings, we recorded 21 woody plant species, including four alien species. We counted from 5 to 2594 saplings on particular plots with an average of 142 ± 270 individuals. We counted from 0 to 243 seedlings on particular plots with an average of 13 ± 35 individuals. The stand age on our plots varied from 42 to 139 years old for *Quercus* spp. stands and from 42 to 117 years old for *P. sylvestris* stands. The mean total aboveground biomass for nutrient-poor sites with *P. sylvestris* was very similar between control plots (187.17 ± 34.50 Mg ha^{-1}) and plots with *P. serotina* (196.99 ± 33.25 Mg ha^{-1}) and *R. pseudoacacia* (182.14 ± 31.44 Mg ha^{-1}). In the case of the *Quercus* spp. stands the average total aboveground biomass of the control stand (278.74 ± 100.16 Mg ha^{-1}) was similar to the stand with *P. serotina* (267.52 ± 93.24 Mg ha^{-1}) but stands with *R. pseudoacacia* (317.01 ± 141.48 Mg ha^{-1}) had slightly higher biomass (Table 1). The differences between *P. serotina* and *R. pseudoacacia* were visible in their biomass. For *P. serotina* we reached aboveground biomass from 0.18 to 47.11 Mg ha^{-1} with an average of 7.34 ± 8.75 Mg ha^{-1} on nutrient-poor sites with *P. sylvestris* and from 0.19 to 27.39 Mg ha^{-1} with an average of 6.68 ± 7.24 Mg ha^{-1} on nutrient-rich sites with *Quercus* spp. For *R. pseudoacacia*, we reached aboveground biomass from 0.22 to 153 Mg ha^{-1} with an average of 20.91 ± 31.69 Mg ha^{-1} on nutrient-poor sites with *P. sylvestris* and from 0.82 to 278.24 Mg ha^{-1} with an average of 50.77 ± 70.37 Mg ha^{-1} on nutrient-rich sites with *Quercus* spp. (Table 1, Fig. 4). *Prunus serotina* occurred only in the understory and subcanopy layers. The largest measured individual of *P. serotina* reached a DBH of 31.1 cm and a height of 19.0 m. *Robinia pseudoacacia* occurred in the understory, subcanopy, and canopy layers. The largest *R. pseudoacacia* individuals reached a DBH of 64.2 cm and a height of 32.0 m.

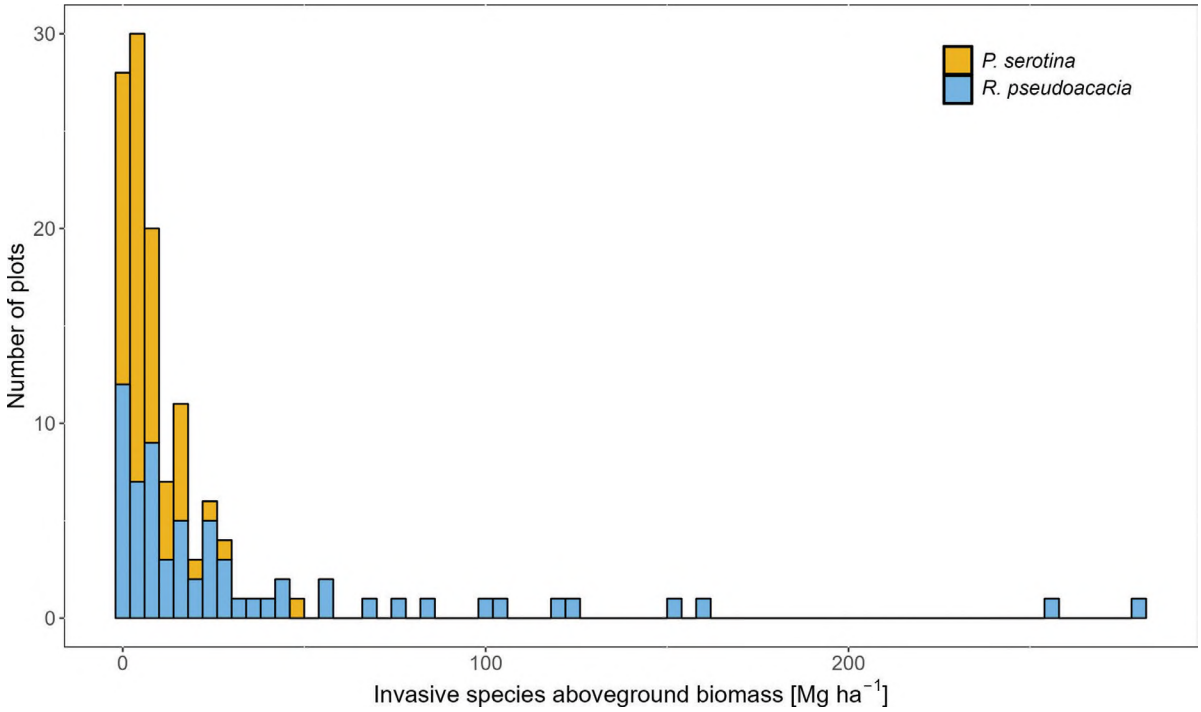

Figure 4. Histogram showing the distribution of invasive species aboveground biomass [Mg ha^{-1}] in plots with *P. serotina* (n = 64), and plots with *R. pseudoacacia* (n = 64). In this graph we excluded control plots (n = 32) with no studied invasive species for clarity.

Relationship between the biomass of invasive trees on species composition the natural regeneration species composition (CCA)

Species composition depended on invader biomass, both for stands with *P. serotina* and *R. pseudoacacia*, and both on the nutrient-rich and nutrient-poor sites. The stand age was statistically significant for *R. pseudoacacia* on nutrient-poor (p = 0.004 Fig. 5, Table 2) and nutrient-rich sites (p = 0.034). *Prunus serotina* biomass was positively correlated with the frequency of *Sorbus aucuparia*, *P. serotina*, *Fagus sylvatica*, and *Q. robur* on nutrient-poor sites, and *A. platanoides*, *Fraxinus excelsior*, *Q. robur*, *Prunus cerasifera*, *Prunus padus*, *P. serotina*, *F. alnus*, *U. minor* and *Sambucus nigra* on nutrient-rich sites. *Robinia pseudoacacia* biomass was positively correlated with *S. aucuparia*, *R. pseudoacacia*, and *S. nigra* on nutrient-poor sites, and *R. pseudoacacia*, *A. platanoides*, *Acer campestre*, *Acer pseudoplatanus*, *U. minor*, *F. alnus*, *P. serotina*, *P. cerasifera*, *C. avellana*, *Euonymus europaeus*, and *S. nigra* on nutrient-rich sites (Fig. 5).

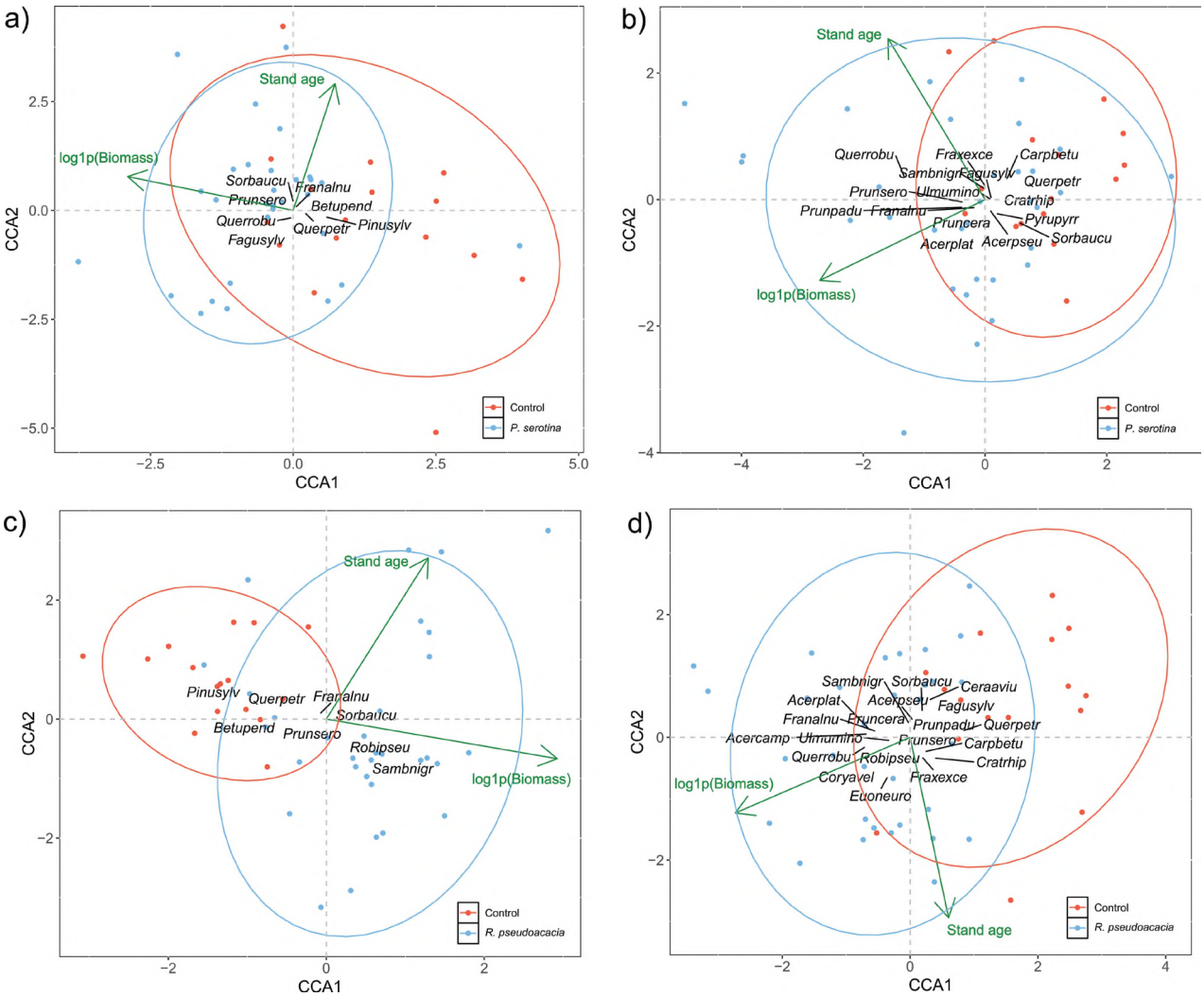

Figure 5. Canonical Correspondence Analysis (CCA) for **a** nutrient-poor sites with *P. serotina* (n = 47 plots) **b** nutrient-rich sites with *P. serotina* (n = 48 plots) **c** nutrient-poor sites with *R. pseudoacacia* (n = 48 plots) **d** nutrient-rich sites with *R. pseudoacacia* (n = 48 plots). Species with a frequency > 20% are labeled. Green arrows and green labels represent environmental variables. Red dots = control plots, light blue dots = plots with *P. serotina* or *R. pseudoacacia*. Abbreviations: log1p(Biomass) — natural logarithm of invader aboveground biomass.

Table 2. Results of permutation-based ANOVA-like test (999 iterations) of constraints significance for CCA. Abbreviations: log1p(Biomass) — natural logarithm of invader aboveground biomass.

	Df	χ^2	F	Pr(>F)
P. serotina nutrient-poor sites (n = 47 plots)				
log1p(Biomass)	1	0.0791	1.6678	0.038
Stand age	1	0.0552	1.1635	0.376
Residual	44	2.0870		
P. serotina nutrient-rich sites (n = 48 plots)				
log1p(Biomass)	1	0.1446	1.9633	0.005
Stand age	1	0.1048	1.4232	0.119
Residual	45	3.3133		
R. pseudoacacia nutrient-poor sites (n = 48 plots)				
log1p(Biomass)	1	0.2372	3.1398	0.001
Stand age	1	0.1725	2.2833	0.004
Residual	45	3.3991		
R. pseudoacacia nutrient-rich sites (n = 48 plots)				
log1p(Biomass)	1	0.1753	2.3626	0.001
Stand age	1	0.1201	1.6184	0.034
Residual	45	3.3382		

Abbreviations: **Df** – degrees of freedom; **χ^2** – Chi-squared statistics; **F** – F-statistics; **Pr(>F)** – p-values.

Threshold Indicator Taxa Analysis

For *P. serotina*, we observed similar trends on both nutrient-poor and nutrient-rich sites (Fig. 6a, b, Suppl. material 1: tables S5, S6). The analysis revealed that *Q. petraea* saplings density declined with increasing *P. serotina* biomass and the opposite trend for *P. serotina* saplings. In the stands with *R. pseudoacacia*, more species revealed any response (Fig. 6c, d, Suppl. material 1: tables S7, S8). The decliners were *Pinus sylvestris*, *Q. petraea*, and *B. pendula* on nutrient-poor sites and *Q. petraea* on nutrient-rich sites. On the nutrient-poor sites *S. nigra*, *P. padus*, *A. platanoides*, and *R. pseudoacacia* increased their saplings density with increasing *R. pseudoacacia* biomass. On the nutrient-rich sites *A. platanoides*, *Q. robur*, and *R. pseudoacacia* increased their saplings density with increasing *R. pseudoacacia* biomass (Fig. 6c, d, Suppl. material 1: tables S7, S8).

Generalized linear mixed-effect models (GLMMs)

Prunus serotina on nutrient-poor sites

The density of all alien species saplings (without *P. serotina*) decreased from 2.3 ± 1.3 in control plots to 0.2 ± 1.3 in stands with 16 Mg ha^{-1} of *P. serotina*. Three species decreased their density with increasing *P. serotina* aboveground biomass. We found the highest effect size for *Q. petraea*. The number of individuals decreased from 24.3 ± 0.3 in control plots to 9.9 ± 0.4 in stands with 16 Mg ha^{-1} of *P. serotina*. *Pinus sylvestris* and *Q. robur* also reacted negatively but with smaller effect sizes. *Pinus sylvestris* individuals decreased from 1.7 ± 1.2 in control plots to 0.4 ± 1.2 in stands with 16 Mg ha^{-1} of *P. serotina*. *Quercus robur* individuals decreased from 0.7 ± 2.2 in control plots to 0.0 ± 2.3 in stands with 16 Mg ha^{-1} of *P. serotina*. Three species increased their density with increasing *P. serotina* aboveground biomass. *Prunus serotina* regenerated the best. The number of its individuals increased from

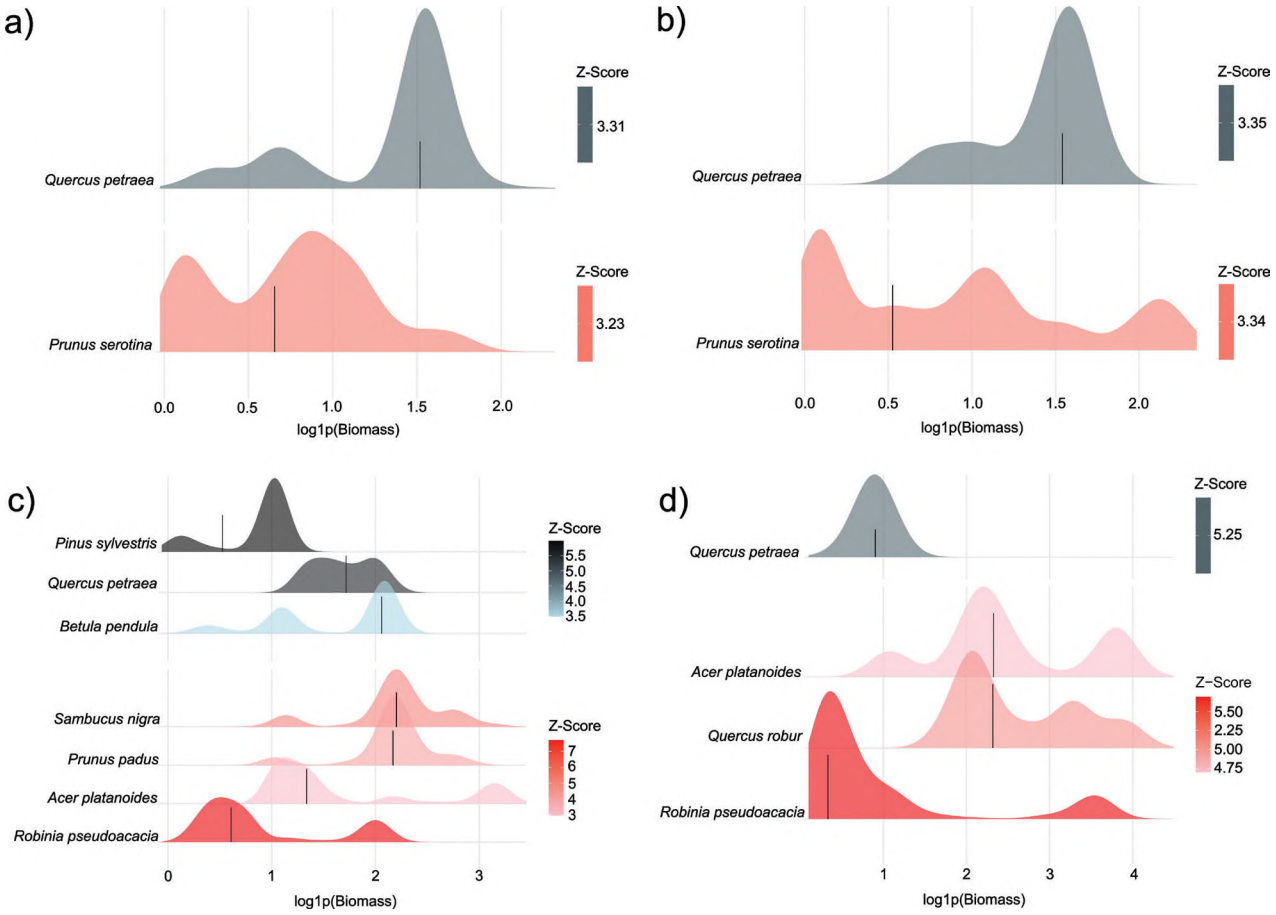

Figure 6. Results of Threshold Indicator Taxa Analysis (see Methods section for interpretation of the graph) for **a** nutrient-poor sites with *P. serotina* (n = 47 plots) **b** nutrient-rich sites with *P. serotina* (n = 48 plots) **c** nutrient-poor sites with *R. pseudoacacia* (n = 48 plots) **d** nutrient-rich sites with *R. pseudoacacia* (n = 48 plots). Grey/blue density estimators represent species responding negatively to invader biomass gradient (decliners) while red color – positively (increasers). We included here only responses for species that were both reliable (reliability ≥ 0.95) and pure (purity ≥ 0.95). For statistics of all species see Suppl. material 1: tables S5–S8.

10.0 ± 0.3 in control plots to 275.6 ± 0.3 in stands with 16 Mg ha^{-1} of *P. serotina*. The other increasers were *S. aucuparia* and *B. pendula* (Table 3, Suppl. material 1: table S9, Fig. 7). We found an increasing number of *P. serotina* and *Q. petraea* seedlings and decreasing number of *P. sylvestris* seedlings with an increase in *P. serotina* aboveground biomass (Table 3, Suppl. material 1: table S14, Fig. 8).

Prunus serotina on nutrient-rich sites

Saplings of two species decreased their density with increasing *P. serotina* aboveground biomass. We observed the highest effect size for *Q. petraea*. The number of individuals decreased from 3.5 ± 2.0 in control plots to 0.2 ± 2.0 in stands with 28 Mg ha^{-1} of *P. serotina*. *Carpinus betulus* was the second decliner, but with a lower effect size. The number of individuals decreased from 1.3 ± 0.8 in control plots to 0.6 ± 0.8 in stands with 28 Mg ha^{-1} of *P. serotina*. Four species increased their density with increasing *P. serotina* aboveground biomass. Similarly to the nutrient-poor sites, *P. serotina* regenerated the best. The number of individuals increased from 2.5 ± 0.6 in control plots to 90.0 ± 0.6 in stands with 28 Mg ha^{-1} of *P. serotina*. The other increasers, but with lower effect sizes, were *F. excelsior*, *U. minor*, and *P. padus* (Table 4, Suppl. material 1: table S10,

Fig. 9). We found an increasing number of *P. serotina* and *A. pseudoplatanus* seedlings with an increase in *P. serotina* aboveground biomass (Table 4, Suppl. material 1: table S15, Fig. 10).

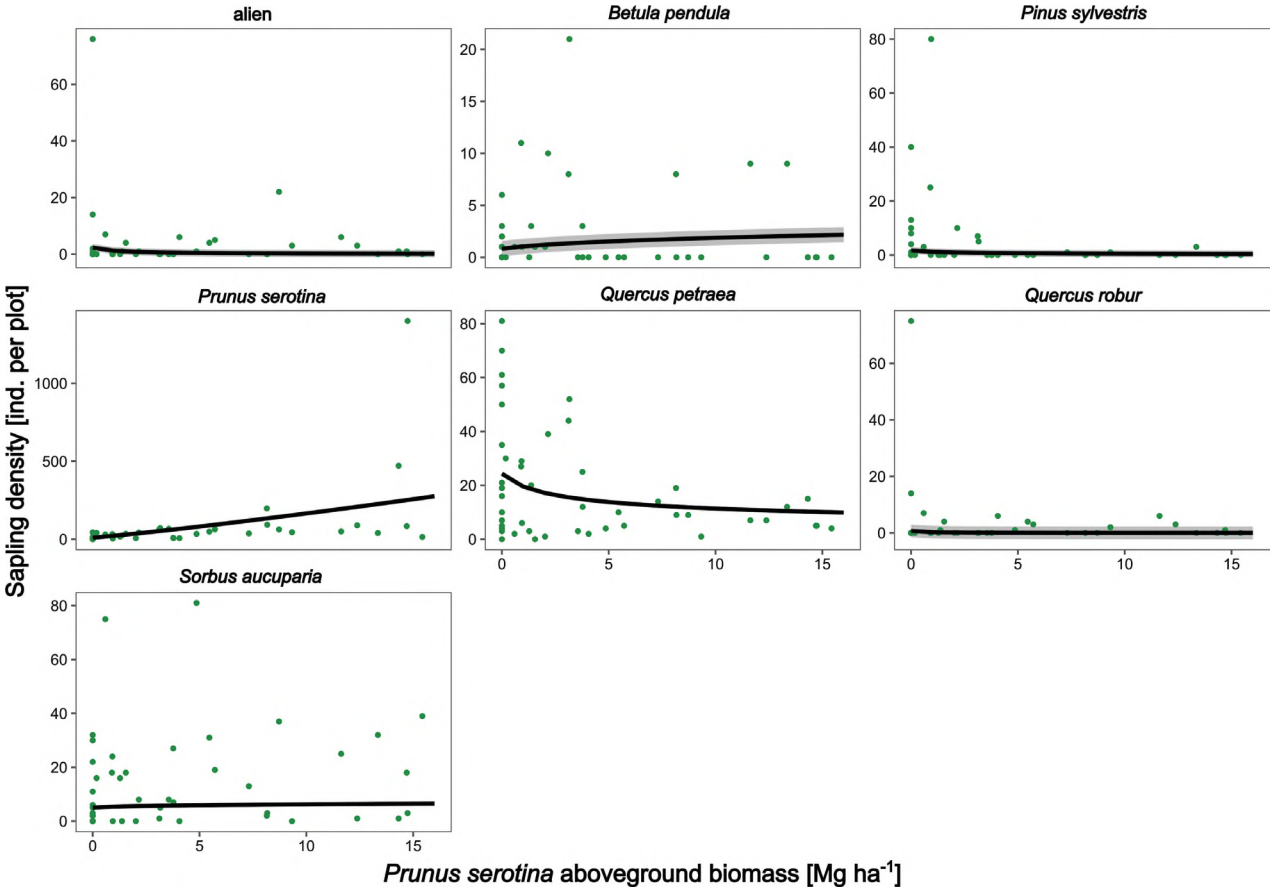

Figure 7. Generalized linear mixed-effect models for sapling density [ind. per plot] of particular species depending on *Prunus serotina* aboveground biomass [Mg ha^{-1}] in nutrient-poor sites. Dark green dots — observed values, black line — marginal responses, grey area — marginal responses ± standard error, alien — density of all alien species saplings excluding *P. serotina*.

Table 3. Predictions of natural regeneration density [ind. per plot] along *P. serotina* aboveground biomass gradient on the nutrient-poor sites, estimated using Generalized Linear Mixed-effect Models. The predicted values are marginal responses from models (Suppl. material 1: tables S9, S14), assuming constant (mean) stand age and excluding random effects.

Species	*P. serotina* aboveground biomass [Mg ha^{-1}]									
	0		2		6		10		16	
	Estimate	SE	Estimate	SE	Estimate	SE	Estimate	SE	Estimate	SE
SAPLINGS										
All alien species (without *P. serotina*)	2.3	1.3	0.8	1.3	0.4	1.3	0.3	1.3	0.2	1.3
Quercus petraea	24.3	0.3	17.2	0.3	13.1	0.3	11.4	0.3	9.9	0.4
Quercus robur	0.7	2.2	0.1	2.2	0.0	2.2	0.0	2.2	0.0	2.3
Pinus sylvestris	1.7	1.2	1.0	1.2	0.6	1.2	0.5	1.2	0.4	1.2
Prunus serotina	10.0	0.3	36.2	0.2	97.6	0.2	165.6	0.2	275.6	0.3
Sorbus aucuparia	5.1	0.7	5.6	0.7	6.0	0.7	6.3	0.7	6.5	0.7
Betula pendula	0.8	0.8	1.2	0.7	1.6	0.7	1.9	0.7	2.2	0.7
SEEDLINGS										
Prunus serotina	1.2	1.1	3.6	1.1	8.2	1.1	12.9	1.1	19.7	1.1
Pinus sylvestris	1.0	0.6	0.7	0.6	0.5	0.6	0.4	0.7	0.3	0.7
Quercus petraea	0.1	1.0	0.2	0.9	0.4	0.9	0.7	0.9	1.0	0.9

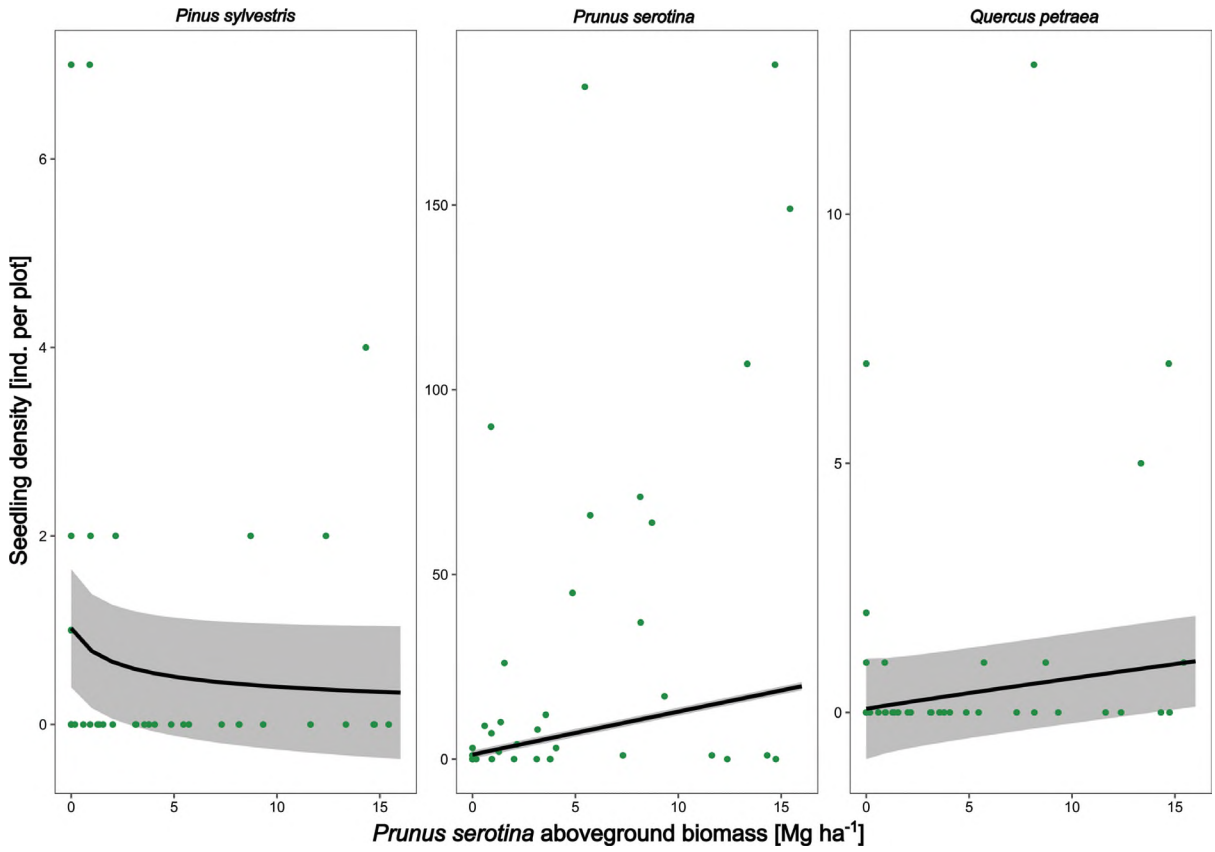

Figure 8. Generalized linear mixed-effect models for seedling density [ind. per plot] of particular species depending on *Prunus serotina* aboveground biomass [Mg ha^{-1}] in nutrient-poor sites. Dark green dots — observed values, black line — marginal responses, grey area — marginal responses ± standard error.

Table 4. Predictions of natural regeneration density [ind. per plot] along *P. serotina* aboveground biomass gradient on the nutrient-rich sites, estimated using Generalized Linear Mixed-effect Models. The predicted values are marginal responses from models (Suppl. material 1: tables S10, S15), assuming constant (mean) stand age and excluding random effects.

Species	*P. serotina* aboveground biomass [Mg ha^{-1}]									
	0		4		10		18		28	
	Estimate	SE	Estimate	SE	Estimate	SE	Estimate	SE	Estimate	SE
SAPLINGS										
Quercus petraea	3.5	2.0	0.9	2.0	0.5	2.0	0.3	2.0	0.2	2.0
Carpinus betulus	1.3	0.8	0.9	0.8	0.7	0.8	0.6	0.8	0.6	0.8
Prunus serotina	2.5	0.6	13.7	0.6	31.9	0.6	57.2	0.6	90.0	0.6
Fraxinus excelsior	2.6	0.8	10.4	0.8	20.5	0.8	32.8	0.8	47.2	0.8
Ulmus minor	0.2	1.0	0.4	1.0	0.6	1.0	0.8	1.0	1.1	1.0
Prunus padus	0.3	1.0	1.7	1.0	3.9	1.0	6.9	1.0	10.9	1.0
SEEDLINGS										
Prunus serotina	0.3	1.0	1.7	1.0	3.9	1.0	6.9	1.0	10.8	1.0
Acer pseudoplatanus	0.3	1.0	1.7	1.0	3.9	1.0	6.9	1.0	10.8	1.0

Robinia pseudoacacia on nutrient-poor sites

The number of all alien species saplings (without *R. pseudoacacia*) increased from 3.2 ± 0.3 in control plots to 21.3 ± 0.3 in stands with 116 Mg ha^{-1} of *R. pseudoacacia*. The number of *S. aucuparia* individuals increased from 7.8 ± 0.3 in control plots to 13.3 ± 0.3 in stands with 116 Mg ha^{-1} of *R. pseudoacacia*. The number of *Q. petraea* individuals decreased from 12.5 ± 0.5 in control plots to 0.9 ± 0.5 in stands with

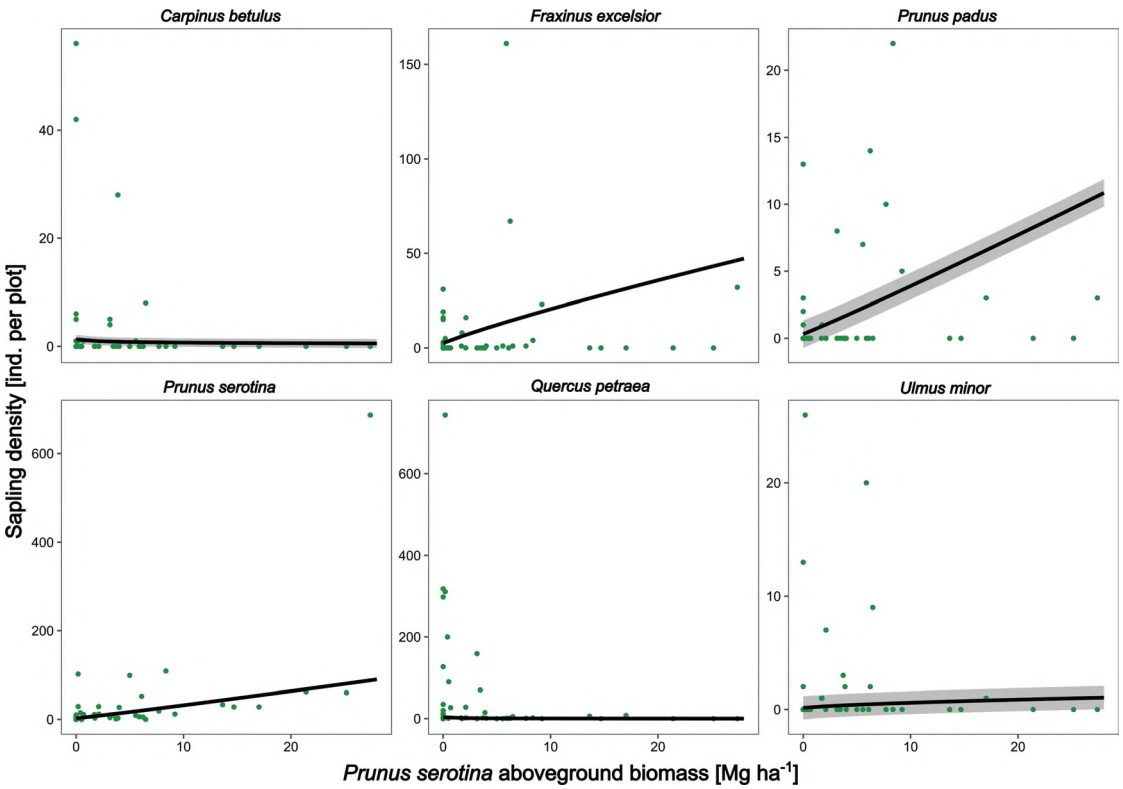

Figure 9. Generalized linear mixed-effect models for sapling density [ind. per plot] of particular species depending on *Prunus serotina* aboveground biomass [Mg ha^{-1}] in nutrient-rich sites. Dark green dots — observed values, black line — marginal responses, grey area — marginal responses ± standard error.

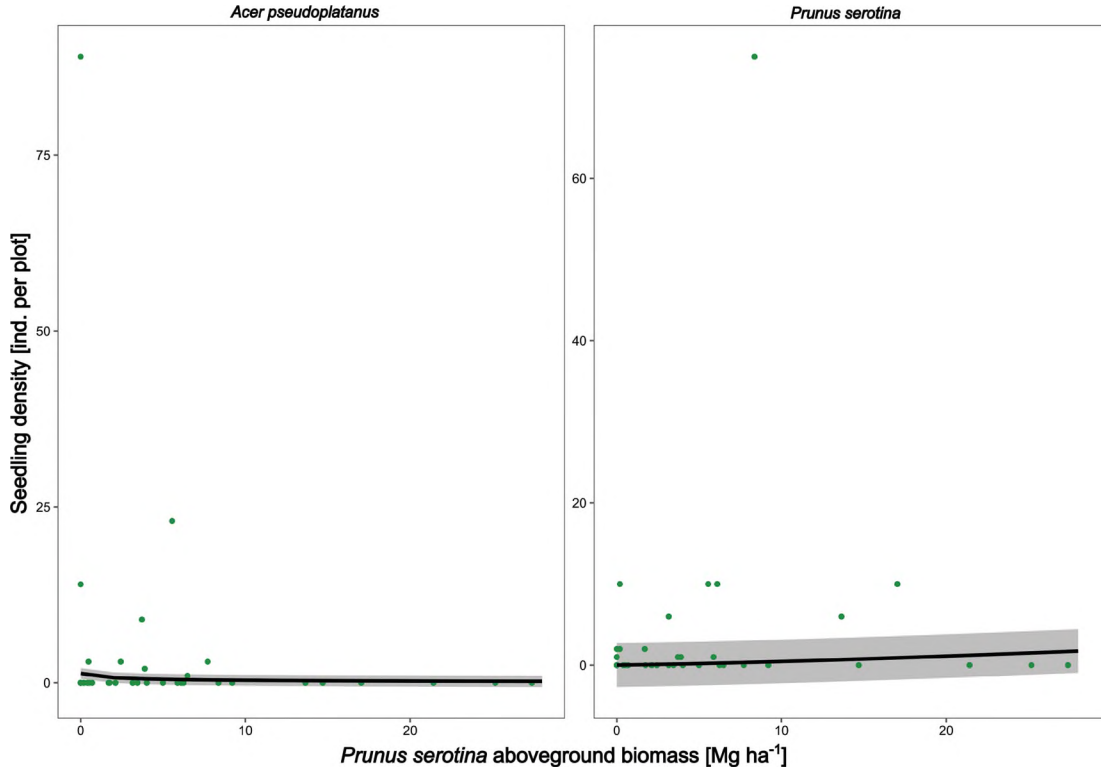

Figure 10. Generalized linear mixed-effect models for seedling density [ind. per plot] of particular species depending on *Prunus serotina* aboveground biomass [Mg ha^{-1}] in nutrient-rich sites. Dark green dots — observed values, black line — marginal responses, grey area — marginal responses ± standard error.

116 Mg ha^{-1} of *R. pseudoacacia*. For *R. pseudoacacia* saplings, we found significant results for the relationship with aboveground biomass for the zero-inflation model, showing that a higher quantity of *R. pseudoacacia* in the stand was negatively correlated with *R. pseudoacacia* regeneration (Estimate = -2.1411, p < 0.001) (Table 5, Suppl. material 1: table S11, Fig. 11). We found an increasing number of *R. pseudoacacia* seedlings and a decreasing number of *P. sylvestris* seedlings with an increase in *R. pseudoacacia* aboveground biomass (Table 5, Suppl. material 1: table S16, Fig. 12).

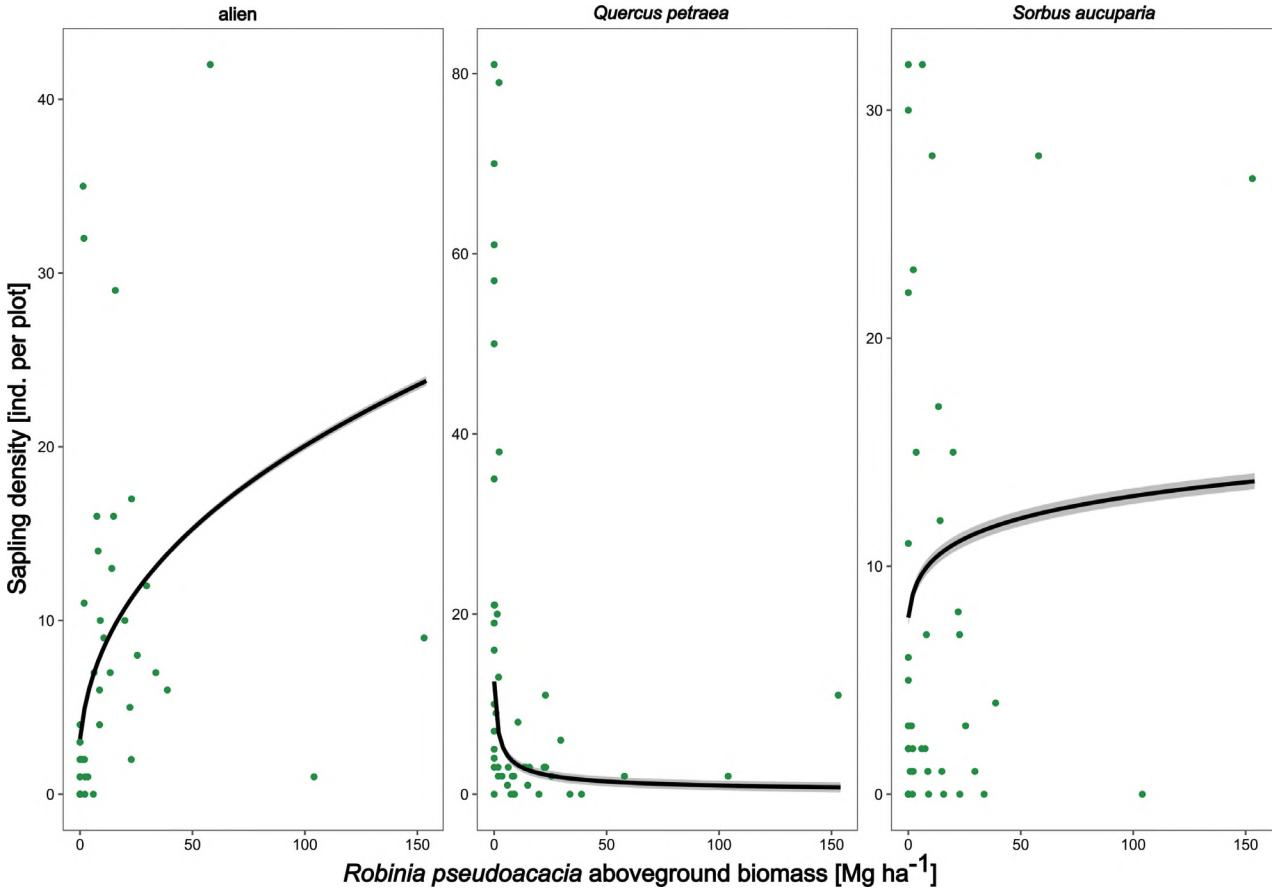

Figure 11. Generalized linear mixed-effect models for sapling density [ind. per plot] of particular species depending on *R. pseudoacacia* aboveground biomass [Mg ha^{-1}] in nutrient-poor sites. Dark green dots — observed values, black line — marginal responses, grey area — marginal responses ± standard error, alien — density of all alien species saplings excluding *R. pseudoacacia*.

Table 5. Predictions of natural regeneration density [ind. per plot] along *R. pseudoacacia* aboveground biomass gradient on the nutrient-poor sites, estimated using Generalized Linear Mixed-effect Models. The predicted values are marginal responses from models (Suppl. material 1: tables S11, S16), assuming constant (mean) stand age and excluding random effects.

Species	*R. pseudoacacia* aboveground biomass [Mg ha^{-1}]									
	0		20		38		78		116	
	Estimate	SE	Estimate	SE	Estimate	SE	Estimate	SE	Estimate	SE
SAPLINGS										
All alien species (without *R. pseudoacacia*)	3.2	0.3	10.7	0.2	13.7	0.2	18.2	0.2	21.3	0.3
Quercus petraea	12.5	0.5	2.3	0.5	1.7	0.5	1.1	0.5	0.9	0.5
Sorbus aucuparia	7.8	0.3	10.9	0.3	11.7	0.3	12.7	0.3	13.3	0.3
SEEDLINGS										
Robinia pseudoacacia	0.0	2.0	0.1	2.0	0.2	2.0	0.4	2.0	0.5	2.0
Pinus sylvestris	0.2	1.2	0.1	1.2	0.1	1.2	0.1	1.3	0.1	1.3

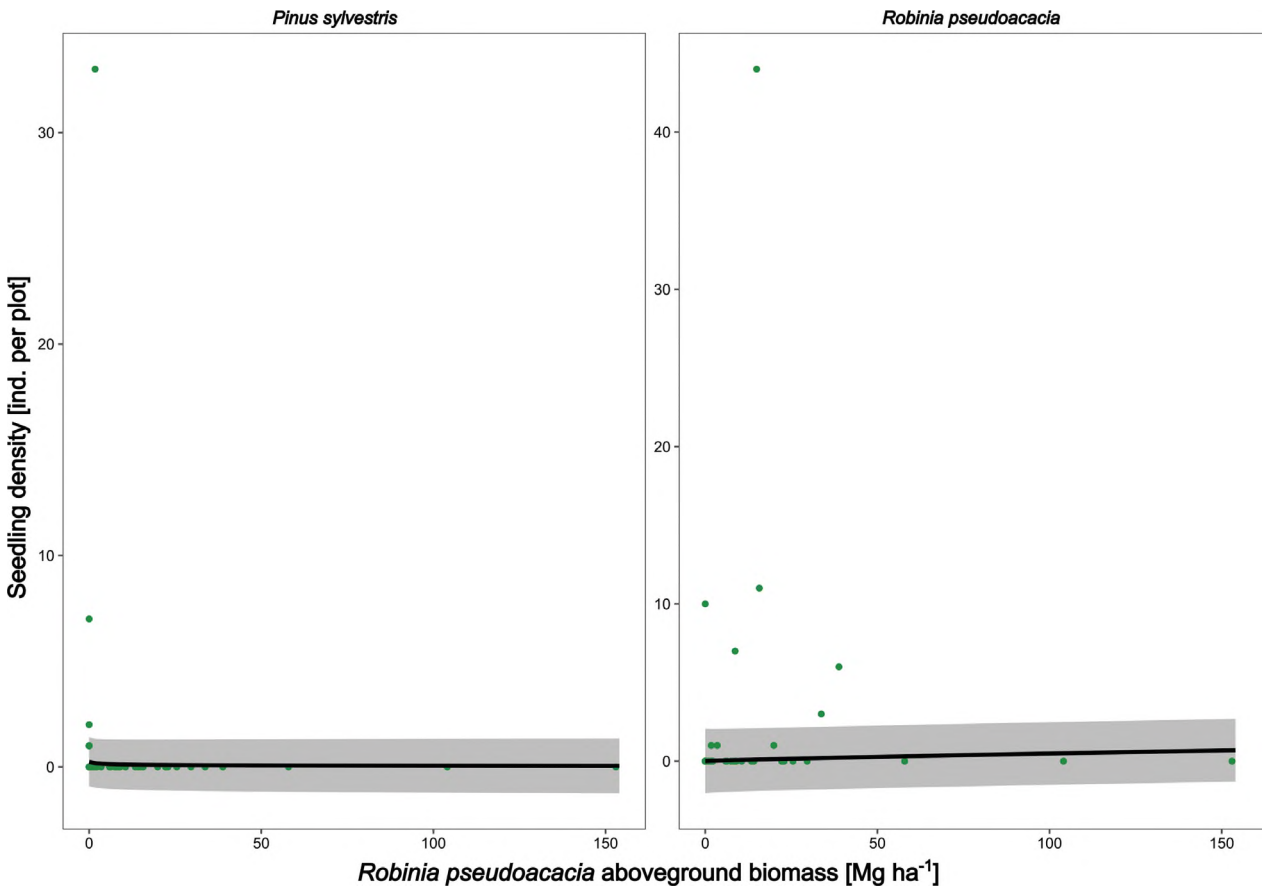

Figure 12. Generalized linear mixed-effect models for seedling density [ind. per plot] of particular species depending on *R. pseudoacacia* aboveground biomass [Mg ha^{-1}] in nutrient-poor sites. Dark green dots — observed values, black line — marginal responses, grey area — marginal responses ± standard error.

Robinia pseudoacacia on nutrient-rich sites

The density of all alien species saplings (excluding *R. pseudoacacia*) increased from 2.8 ± 0.4 in control plots to 13.0 ± 0.4 in stands with 208 Mg ha^{-1} of *R. pseudoacacia*. Four species decreased their density, and 13 species increased their density with increasing *R. pseudoacacia* aboveground biomass. Mainly forest-forming species like *Q. petraea* and *F. sylvatica* decreased the density of saplings, while species occurring usually as an admixture in the stands (all native *Acer* spp., *F. excelsior*, and *U minor*) and shrubs (*S. nigra*, *C. avellana*, *E. europaeus*, *Crataegus rhipidophylla*, and *F. alnus*) increased their saplings density with increasing *R. pseudoacacia* biomass. We found low negative effects of increasing *R. pseudoacacia* biomass on the saplings of *C. avium* and invasive *P. cerasifera*. Some of the species reached quite high effect sizes. The number of *Q. petraea* individuals decreased from 8.8 ± 0.8 in control plots to 0.1 ± 0.9 in stands with 208 Mg ha^{-1} of *R. pseudoacacia.* The number of *A. pseudoplatanus* individuals increased from 9.5 ± 0.6 in control plots to 36.9 ± 0.6 in stands with 208 Mg ha^{-1} of *R. pseudoacacia*. The number of *F. excelsior* individuals increased from 15.0 ± 0.7 in control plots to 36.8 ± 0.8 in stands with 208 Mg ha^{-1} of *R. pseudoacacia.* The number of *S. nigra* individuals increased from 1.8 ± 0.6 in control plots to 10.9 ± 0.6 in stands with 208 Mg ha^{-1} of *R. pseudoacacia* (Table 6, Suppl. material 1: table S12, Fig. 13). We found a decreasing number of *Q. petraea* and *A. pseudoplatanus* seedlings with an increase in *R. pseudoacacia* aboveground biomass (Table 6, Suppl. material 1: table S17, Fig. 14).

Table 6. Predictions of natural regeneration density [ind. per plot] along *R. pseudoacacia* aboveground biomass gradient on the nutrient-rich sites, estimated using Generalized Linear Mixed-effect Models. The predicted values are marginal responses from models (Suppl. material 1: tables S12, S17), assuming constant (mean) stand age and excluding random effects.

Species	*R. pseudoacacia* aboveground biomass [Mg ha^{-1}]									
	0		34		70		138		208	
	Estimate	SE	Estimate	SE	Estimate	SE	Estimate	SE	Estimate	SE
SAPLINGS										
All alien species (without *R. pseudoacacia*)	2.8	0.4	7.8	0.3	9.5	0.3	11.6	0.4	13.0	0.4
Quercus petraea	8.8	0.8	0.4	0.8	0.2	0.8	0.1	0.9	0.1	0.9
Fagus sylvatica	1.0	0.6	0.2	0.6	0.2	0.7	0.1	0.8	0.1	0.8
Cerasus avium	0.5	1.1	0.0	1.3	0.0	1.4	0.0	1.5	0.0	1.5
Prunus cerasifera	0.4	2.6	0.1	2.6	0.1	2.6	0.1	2.6	0.1	2.6
Robinia pseudoacacia	1.1	0.7	2.7	0.7	3.1	0.7	3.7	0.7	4.1	0.7
Prunus serotina	0.6	0.6	2.8	0.6	3.8	0.6	5.1	0.6	6.1	0.6
Quercus robur	0.0	1.5	0.2	1.4	0.2	1.4	0.3	1.5	0.3	1.5
Acer pseudoplatanus	9.5	0.6	23.4	0.6	28.0	0.6	33.3	0.6	36.9	0.6
Acer platanoides	0.1	0.9	2.0	0.9	3.6	0.9	6.3	0.9	8.9	0.9
Acer campestre	0.1	2.4	0.4	2.4	0.5	2.4	0.7	2.4	0.9	2.4
Fraxinus excelsior	15.0	0.7	27.3	0.7	30.7	0.7	34.4	0.8	36.8	0.8
Ulmus minor	0.4	1.0	1.3	1.0	1.7	1.0	2.1	1.0	2.5	1.0
Sambucus nigra	1.8	0.6	6.0	0.6	7.6	0.6	9.5	0.6	10.9	0.6
Corylus avellana	0.2	0.5	0.9	0.3	1.2	0.4	1.6	0.4	1.9	0.4
Euonymus europaeus	0.0	1.1	0.4	1.1	0.5	1.0	0.8	1.1	1.1	1.1
Crataegus rhipidophylla	0.1	1.1	0.3	1.0	0.4	1.0	0.6	1.0	0.7	1.0
Frangula alnus	0.1	1.5	0.3	1.5	0.4	1.5	0.4	1.5	0.5	1.5
SEEDLINGS										
Quercus petraea	0.1	1.8	0.0	1.8	0.0	1.8	0.0	1.9	0.0	1.9
Acer pseudoplatanus	0.6	1.5	0.1	1.5	0.0	1.5	0.0	1.6	0.0	1.6

Comparison of the methods

We used three different types of analyses, and in almost all cases we reached consistent results (Table 7). Among three tested methods we found the most consistent relationships for *Q. petraea* in all variants and *P. serotina* in plots with *P. serotina*. According to the Threshold Indicator Taxa Analysis, on the nutrient-poor sites with *P. serotina*, *B. pendula* were correlated negatively with the invader biomass, but according to the GLMMs positively. We found a contrast pattern in the case of *R. pseudoacacia* regeneration in stands with *R. pseudoacacia*, as TITAN2 suggested a positive relationship, but the model suggested a negative (but only for the zero-inflation component).

Discussion

General patterns

Observational studies on the impact of invasive species on various ecosystems, including forests, should not be considered as a simple causation based on observed correlations. Ecosystems are very complex and each of their elements is simultaneously affected by various factors. Impact assessment should be multidimensional and a systemic approach. In our plots we observed different densities of saplings and seedlings of individual species. We refer to individual hypotheses in the

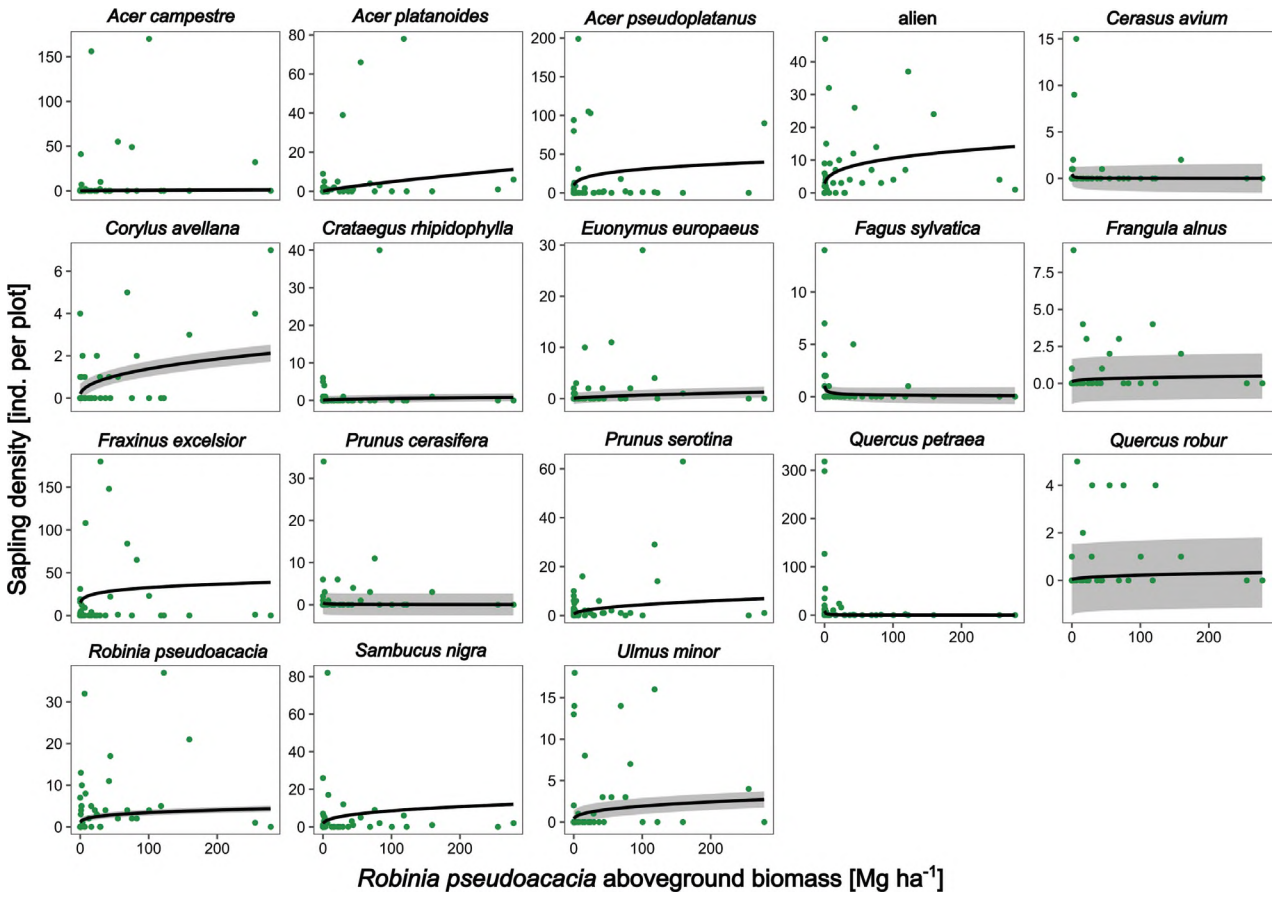

Figure 13. Generalized linear mixed-effect models for sapling density [ind. per plot] of particular species depending on *R. pseudoacacia* aboveground biomass [Mg ha^{-1}] in nutrient-rich sites. Dark green dots — observed values, black line — marginal responses, grey area — marginal responses ± standard error, alien — density of all alien species saplings excluding *R. pseudoacacia*.

following sections of the discussion. The relationship between natural regeneration density and biomass of *P. serotina* and *R. pseudoacacia* can be both positive or negative, and this is in line with recent studies showing that results depend on the environmental context (Sapsford et al. 2020; Catford et al. 2022) and the reference ecosystem used for comparison (Sádlo et al. 2017; Medvecká et al. 2018; Dyderski and Jagodziński 2021b). Our study improves the knowledge about the relationship between different invasive tree biomasses and ecosystem services.

Species-specific patterns

We found different relationships between particular species natural regeneration densities and *R. pseudoacacia* and *P. serotina* biomasses (H1, H2). We confirm both the first (H1) and second (H2) hypotheses. The biomass of *R. pseudoacacia* was correlated with the density of natural regeneration more than *P. serotina* (H1). We also confirm the second hypothesis, as individual natural regeneration species showed different patterns of density. Some showed a decrease in density with the biomass increase of invaders, others showed opposite trends. Differences between individual species were seen in the number of individuals in each quantity of the invasive species, the shape (more linear or exponential), and the slope of the curves in the models. Similarly, in TITAN2, we found differences in the number of species and shapes of ridges (H2). Some natural regeneration species revealed

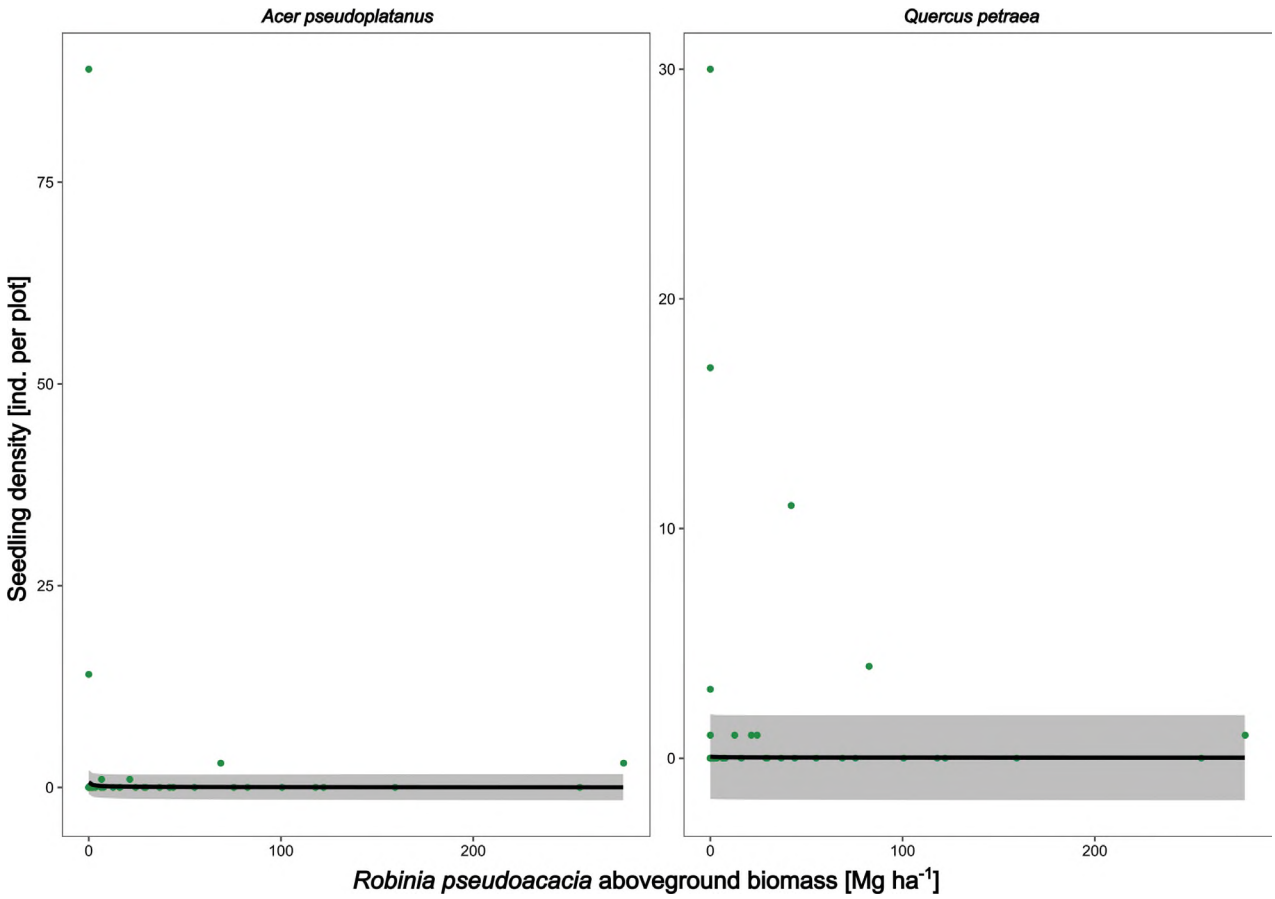

Figure 14. Generalized linear mixed-effect models for seedling density [ind. per plot] of particular species depending on *R. pseudoacacia* aboveground biomass [Mg ha^{-1}] in nutrient-rich sites. Dark green dots — observed values, black line — marginal responses, grey area — marginal responses ± standard error.

positive relationships with invader biomass (mostly *P. serotina* in the stand with *P. serotina*) and some negative (*Q. petraea*, *P. sylvestris*). Those differences between particular species relationship with *R. pseudoacacia* or *P. serotina* should be mostly connected with different light or nutrient requirements of particular sapling and seedling species. As the transformations of both studied neophytes changed along their biomasses, also the density of particular natural regeneration species should change more intensively. There are visible trends connected with the ecological niches of particular trees, but they should be interpreted with caution. More shade-tolerant and nitrophilous species increased their abundances with invader biomass increasing, e.g., *F. excelsior* or *Acer* spp. In contrast, light-demanding and acidophilous *P. sylvestris* decreased its abundance or the abundance remained unchanged. Increasing biomass of either *P. serotina* or *R. pseudoacacia* led to reduced light availability on the forest floor and higher nutrient content in the soil (Rice et al. 2004; Dyderski and Jagodziński 2019; Engel et al. 2024). Those transformations did not support *P. sylvestris* regarding natural regeneration growth, in both saplings and seedlings. Lázaro-Lobo et al. (2021) also mentioned that the response of a particular species' natural regeneration depends on their functional traits, and the competition between invasive tree species with desirable species depends on their niche spacing. There are also visible differences in the number of significant relationships between sapling species densities and *R. pseudoacacia* or *P. serotina* biomasses (H1). Focusing only on GLMMs (Table 7), in nutrient-rich habitats

Table 7. Summary of saplings species' responses to invasive trees according to different analyses. CCA based on species with frequency > 20%, TITAN2 based on species with purity and reliability >= 0.95. GLMMs based on statistically significant results for the effect of invader aboveground biomass.

	Prunus serotina						*Robinia pseudoacacia*					
	Poor sites			Rich sites			Poor sites			Rich sites		
	C	T	M	C	T	M	C	T	M	C	T	M
Acer campestre										+		+
Acer platanoides				+				+		+	+	+
Acer pseudoplatanus				−						+		+
Betula pendula	−		+				−	−				
Corylus avellana										+		+
Cerasus avium										−		−
Carpinus betulus				−		−				−		
Crataegus rhipidophylla				−						−		+
Euonymus europaeus										+		+
Frangula alnus	−			+			+			+		+
Fraxinus excelsior				+		+				−		+
Fagus sylvatica	+			?						−		−
Prunus cerasifera				+						+		−
Prunus padus				+		+		+		−		
Pyrus pyraster				−								
Prunus serotina	+	+	+	+	+	+	−			−		+
Pinus sylvestris	−		−				−	−				
Quercus petraea	−	−	−	−	−	−	−	−	−	−	−	−
Quercus robur	+		−	+						+	+	+
Robinia pseudoacacia							+	+	−	+	+	+
Sorbus aucuparia	+		+	−			+		+	−		
Sambucus nigra				+			+	+		+		+
Ulmus minor				+		+				+		+

Abbreviations: **C** — Canonical Correspondence Analysis (CCA); **T** — Threshold Indicator Taxa Analysis (TITAN2); **M** — Generalized Linear Mixed-Effect Models (GLMMs); + — positive effect of invasive species; − — negative effect of invasive species; ? — unclear effect of invasive species.

17 species (13 positively and four negatively) responded significantly to *R. pseudoacacia* increasing biomass and six (four positively and two negatively) to *P. serotina* increasing biomass. In nutrient-poor habitats, three species (one positively and two negatively) responded to *R. pseudoacacia* increasing biomass and six (three positively and three negatively) to *P. serotina* increasing biomass. According to GLMMs in nutrient-rich habitats (*R. pseudoacacia*: 76%, *P. serotina*: 67%), the share of the number of species reacting positively to the invader's biomass in the number of species that responded significantly positively and negatively was higher than in coniferous habitats nutrient-poor habitats (*R. pseudoacacia*: 33%, *P. serotina*: 50%; H3).

For some species, we observed some trends similar to those observed by Dyderski and Jagodziński (2020), conducted in protected forests of the nearby Wielkopolska National Park. The density of forest tree species was lower in invaded stands by both *R. pseudoacacia* and *P. serotina* than in non-invaded while shrubs and admixed trees increased their density. Our study provided a significant advance from this study, as we included invader abundance, that allows for assessment of various stages of invasion (López-Núñez et al. 2017).

Our observations regarding the negative correlation between invasive trees biomass and the natural regeneration of forest-forming species are in line with the findings of Terwei et al. (2013) and Kowarik et al. (2019). Terwei et al. (2013)

showed that in the hardwood floodplain forests, *R. pseudoacacia* in the stand was positively correlated with the density of *R. pseudoacacia* seedlings. However, *P. serotina* in the stands was positively correlated with *P. serotina* seedlings but negatively with *U. minor* seedlings. Langmaier and Lapin (2020), in their review of the impact of different invasive plant species on forest regeneration, also discussed the impact of *P. serotina* and *R. pseudoacacia*. Based on the works of other authors (e.g., Rahmonov 2009; Maringer et al. 2012; Petrášová et al. 2013; Radtke et al. 2013; Terwei et al. 2013), Langmaier and Lapin (2020) synthesized the negative impact of *R. pseudoacacia* on species e.g., *Q. petraea*, *Q. robur*, *P. sylvestris*, *U. minor*. In our studies, we confirmed a negative correlation of *Q. petraea* and *P. sylvestris* regeneration density with invader biomass. For *Q. robur* and *U. minor*, we obtained less obvious positive responses. *Quercus robur* was less frequent than *Q. petraea* in our plots, while for *U. minor* we obtained significant results only for nutrient-rich sites. However, it should be borne in mind that their work accounted for habitats not only from Central Europe, but also other ecoregions, e.g., Western European deciduous forests, Pannonian mixed forests, or riparian forests.

Ambiguous invasional meltdown and propagule pressure hypotheses

When invasive species arrive in new niches, they can change soil chemicals, transform light conditions, and make the ecosystem more suitable for the other alien species (Crooks 2002; Corenblit et al. 2014; Jagodziński et al. 2024). In the longer term, this may increase the negative impact on biodiversity and other ecosystem services. For the total alien species natural regeneration density, we confirm the invasional meltdown hypothesis (H4) (Simberloff and Holle 1999) only for *R. pseudoacacia*, both on the nutrient-poor and nutrient-rich sites. Since we examined the relationship between *R. pseudoacacia* and *P. serotina* and the total density of all alien species in the regeneration layer, it is impossible to find species-specific patterns related to their biology and ecology. However, for some individual species we obtained significant results. *Prunus serotina* regeneration density was higher in plots with higher *R. pseudoacacia* biomass on nutrient-rich sites. However, little is known about the possible interactions between the adult *R. pseudoacacia* and *P. serotina* natural regeneration and vice versa. The interesting fact was that invasive *P. cerasifera* abundances decreased with an increase in *R. pseudoacacia* aboveground biomass. Due to the similar biology and ecology of this species to *P. serotina* we would expect rather similar responses. Czortek et al. (2024) proved that the presence of *P. cerasifera* natural regeneration is favored by higher light availability. However, this species avoids places with a higher number of functional types, which may indicate its lower resistance to competition than *P. serotina*.

According to the propagule pressure hypothesis, the higher the propagule pressure, the more effective colonization (Lonsdale 1999; Lockwood et al. 2005; Blackburn et al. 2011). This dependence of studied species on propagule pressure was confirmed in numerous previous studies (Vanhellemont et al. 2009; Vítková et al. 2017; Dyderski and Jagodziński 2018). Trees acquire reproductive abilities late. However, they retain these abilities for a very long time. More propagule sources should increase the regeneration capacity. We confirmed this hypothesis for *P. serotina* on both nutrient-rich and nutrient-poor sites, but the predicted values of sapling and seedling densities were higher on nutrient-poor sites. For *R. pseudoacacia*, we confirmed this hypothesis for saplings on nutrient-rich sites and seedlings

on nutrient-poor sites, but the predicted densities were low. In general, in our plots *R. pseudoacacia* did not regenerate as effectively as *P. serotina*. *Robinia pseudoacacia* spreads generatively mostly by wind and therefore prefers open spaces. *Prunus serotina* seeds mostly fall directly into the soil and to a lesser degree are spread by birds (Deckers et al. 2008; Vanhellemont et al. 2009; Dylewski et al. 2017). Also, both *P. serotina* (Starfinger et al. 2003) and *R. pseudoacacia* (Bouteiller et al. 2023) easily regenerate vegetatively by root suckers.

Dependence on habitat context and biotic resistance/acceptance

Biological invasion dynamics can depend on several factors: environmental conditions, interactions between species, anthropogenic factors, and management (González-Moreno et al. 2014; Sapsford et al. 2020; Catford et al. 2022). To exclude the management context, we established study plots in forest patches without visible impacts of silvicultural treatments e.g., planting or removing trees from plots. We also placed them in similar climatic conditions. We expected a more distinct decline in the density of natural regeneration to invader quantity/biomass on nutrient-poor than on nutrient-rich sites (H3) (Chmura 2004; Halarewicz 2011). In general, in nutrient-rich sites, there are higher densities of native trees understory, so the competition with invasive species is stronger. This is indicated by the number of species that reached a frequency > 20%. Comparing the abundances, *P. serotina* was more successful on nutrient-poor than nutrient-rich sites. Results for *P. serotina* are connected with the Empty Niche Hypothesis (Elton 1958; Schmitt 2020). This hypothesis suggests that invasive species can successfully settle new ecosystems by occupying weakly filled or unfilled ecological niches, where native species are less common or absent. In Central Europe, nutrient-poor sites with *P. sylvestris* have lower richness and abundance of native species compared to nutrient-rich habitats. *Prunus serotina* was massively introduced on nutrient-poor sites by foresters (Starfinger et al. 2003; Engel et al. 2024; Nyssen et al. 2024). Small competition from native trees facilitated the spread of *P. serotina* to new stands and led to their dominance in these habitats. This species further spreads easily to nearby stands. Especially, on nutrient-rich sites with *R. pseudoacacia*, we can observe that many of the native tree species regeneration increased their abundance with invader biomass increasing. More shade-tolerant species showed a positive correlation with invader biomass, except for *C. betulus* on nutrient-rich sites with *P. serotina*. This finding contradicts a previous study (Dyderski and Jagodziński 2020) revealing a positive response of this species to *P. serotina* presence. However, in the cited study, this response regarded *P. sylvestris* plantations on nutrient-rich sites, thus it cannot be directly compared. Our results balance between supporting the biotic acceptance (Stohlgren et al. 2006) and biotic resistance (Elton 1958; Levine et al. 2003) hypotheses. In the case of stands with *P. serotina*, both in poor and fertile habitats, the density of its regeneration increased with the biomass of the parental trees, mainly due to the availability of propagules and dispersal mechanisms: barochory and zoochory. Nevertheless, the effect sizes were higher on the poor sites. In the case of *R. pseudoacacia* stands, we observed slightly better regeneration of this species in nutrient-rich habitats. To sum up, for *P. serotina* our results are rather in line with the biotic resistance hypothesis (Elton 1958; Levine et al. 2003), while for *R. pseudoacacia* they rather in line with biotic acceptance (Stohlgren et al. 2006). The more visible relationships between natural regeneration and

invader biomass in nutrient-poor habitats depend on specific ecological conditions, specific plant species composition, and soil fertility. Therefore, any transformation by an invasive species is more severe for the species occurring there.

Three different analyses

We had to adapt the database to the analysis guidelines. CCA was the least conservative analysis in the case of input data. CCA is also the least sensitive on extremal observations. In models, we excluded one plot for *C. betulus* saplings and two plots for *C. avium* saplings (see the rationale in the Materials and Methods section). Thanks to the use of TITAN2, we were able to detect the threshold for particular invasion levels e.g., *P. serotina* saplings reacted quickly with big abundance on even small quantity of *P. serotina* in the stands, while *Q. petraea* as a decliner was more tolerant to *P. serotina* biomass increasing. For *C. avium* omitting these records in the models did not change the trend (positive/negative) but reduced the standard error and smoothed the regression curve. In the case of *C. betulus*, removing the extreme observation changed the trend from positive to negative. The negative trend is consistent with the CCA result. The extreme observation results from the fact that there were adult *C. betulus* in the vicinity of the plot, acting as a propagule source. According to the guidelines of statistical model development, we should remove this outlier. The model after removing the outlier had a more stable distribution of residuals and a lower standard error of estimates. Even though each of the analyses we use is based on slightly different data structures and responds differently to data variability, the results we obtain are very similar. In general, consistent responses revealed by three different methods suggest that all these tools are useful in the assessment of correlations with invasive species biomass. We also found that TITAN2 resulted in the most conservative approach – for *P. serotina* and *R. pseudoacacia* on nutrient-rich sites it revealed relationships only in the cases confirmed by two other methods. For *R. pseudoacacia* on nutrient-poor sites, it revealed relationships not confirmed by two other methods only for three species.

Wider context and management implications

In the context of current trends in forestry, *P. sylvestris* is still the main species in nutrient-poor sites areas, while *Quercus* spp. is in nutrient-rich sites. Therefore, referring to habitats studied here, densities of main forest-forming species were negatively correlated with the biomass of studied invasive species, especially *Q. petraea*. *Prunus serotina* also hindered the regeneration of *P. sylvestris* in the poor sites. We found an increasing density of *Quercus robur* saplings with increasing *R. pseudoacacia* biomass in fertile habitats, but negatively correlated with *P. serotina* biomass in poor habitats. In the context of natural forests and ongoing climate change, the situation looks a bit different. Wide-scale studies predict the retreat of forest-forming tree species from Central Europe, especially *P. sylvestris*, as a response to climate change (Dyderski et al. 2018; Chakraborty et al. 2021; Wessely et al. 2024). That way, studied neophytes can enhance this negative effect by suppressing the natural regeneration of studied species. Recent management strategies propose in some cases the assimilation of invasive species with native ecosystems (Nyssen et al. 2024), also for *P. serotina* (Nyssen and Vanhellemont 2016; Engel et al. 2024) and *R. pseudoacacia* (Sádlo et al. 2017). Such a strategy is recommended especially in fertile habitats that are biotically more resistant

to the development of invasion. In assimilating studied invasive species, managers should be hypersensitive to their potential impacts on main forest-forming species. When we want to maintain or increase the number of species such as *Q. petraea* in the regeneration, we should take into account the results of our research and apply methods that will facilitate their survival. Management in fertile habitats should be adapted to a long-term management plan. If we want to mimic natural processes, the presence of *R. pseudoacacia* (based on our research) may be helpful, as it promotes species such as *F. excelsior*, *U. minor*, or *Acer* spp. On the other hand, if we want to preserve as large a *Quercus* population as possible, some human action may be necessary. In the case of *P. sylvestris* stands, we maintain the fact that if we want successful *P. sylvestris* regeneration, it is necessary to take into account the observed decreasing density of *P. sylvestris* regeneration with both invasive species studied biomass increasing and support the regeneration of *P. sylvestris*. Langmaier and Lapin (2020) summarized that there are studies that indicate that in the case of *R. pseudoacacia*, its eradication measures or adaptation of silvicultural measures are the most frequent management actions, while in the case of *P. serotina* – early detection. The latter concerns both decision-makers and the entire society, because it is easier to control biological invasions in the early stages. In turn, silvicultural treatments can be modified to promote selective cutting, and appropriately manage the closure of tree crowns and density with local reduction of invasive species combined with the promotion of species of native origin. Unfortunately, our study revealed the negative correlations between studied invasive species biomass and the *Q. petraea* natural regeneration in poor sites. Due to changing climatic conditions leading to the retreat of coniferous species, many see the potential of *Q. petraea* to replace *P. sylvestris* (Hanewinkel et al. 2013; Dyderski et al. 2025). Since *R. pseudoacacia* and *P. serotina* are very common in European forests (Wagner et al. 2017; Campagnaro et al. 2018), and are predicted to expand their range under the changing climate (Puchałka et al. 2021, 2023), we may expect the negative impact on *Q. petraea* regeneration, that will require particular attention.

Although our study focused on managed forests, certain relationships can be related to natural forests. The areas we searched had the structure of semi-natural forests, managed in a way that imitated natural processes. In the case of protected forests, it is important to monitor the presence and impact of invasive species on natural processes and prevent possible damage they may cause. Eradication of invasive trees is expensive and sometimes counter-productive or even makes the situation worse (Namura-Ochalska and Borowa 2015; Nyssen and Vanhellemont 2016; Nyssen et al. 2024). Our study should be helpful for stakeholders in making decisions about the assimilation or eradication of invasive trees in particular types of stands on particular habitats (Nyssen and Vanhellemont 2016; Sádlo et al. 2017).

Conclusions

Our study provided the first quantitative assessment of the relationships between invasive tree biomass and forest natural regeneration, along the gradient of invader biomass. Additionally, we compared patterns obtained using three different statistical approaches: ordination, Threshold Indicator Taxa Analysis, and generalized linear mixed-effects models. We confirmed that invader taxa and their biomass are important and differentiate the strength of the relationship with natural regeneration. Additionally, we observed different relationships between nutrient-rich and nutrient-poor sites. Moreover, particular tree species were differently related to invader biomass on

particular sites and with different effect sizes. The most important finding is the negative relationship of studied invasive trees on the regeneration of crucial forest-forming tree species typical of the studied habitats, such as *P. sylvestris* in poor sites and *Q. petraea* in both nutrient-poor and rich sites. In general, *P. serotina* regenerated better than *R. pseudoacacia*, especially on nutrient-poor sites. For both species, we confirmed the importance of propagule pressure, expressed by parental tree biomass. We also confirmed the invasional meltdown hypothesis for stands with *R. pseudoacacia*, as the density of all non-native saplings (excluding *R. pseudoacacia*) increased with an increase in *R. pseudoacacia*. However, we did not confirm this hypothesis for stands with *P. serotina*. We also showed that three tested statistical approaches reveal consistent results, supporting the strength of our conclusions.

The results of our study are crucial for selecting tree species that regeneration is more vulnerable to studied invaders. This knowledge can improve the prioritization of management and designation of forest patches requiring additional silvicultural treatments to maintain or initiate natural regeneration. Moreover, our results allow determining thresholds of invasive biomass at which we observed a decreasing density of natural regeneration of the main tree species. For that reason, our study is important in the managed forests promoting natural regeneration, as well as for the protected forest areas e.g., national parks or forest reserves.

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Additional information

Conflict of interest

The authors declare no conflict of interest. The funders had no role in the design of the study; in the collection, analyses, or interpretation of data; in the writing of the manuscript, or in the decision to publish the results.

Ethical statement

No ethical statement was reported.

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Author contributions

Conceptualization: SB, MKD; methodology: SB, MKD; investigation: SB, MKD; formal analysis: SB; visualization: SB; writing—original draft preparation: SB; writing—review and editing: MKD; funding acquisition: MKD.

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Data availability

All data supporting the results are archived in the figshare repository (Dyderski and Bury 2024) 10.6084/m9.figshare.26809084.

References

Aerts R, Ewald M, Nicolas M, Piat J, Skowronek S, Lenoir J, Hattab T, Garzón-López CX, Feilhauer H, Schmidtlein S, Rocchini D, Decocq G, Somers B, Van De Kerchove R, Denef K, Honnay O (2017) Invasion by the Alien Tree *Prunus serotina* Alters Ecosystem Functions in a Temperate Deciduous Forest. Frontiers in Plant Science 8:179. https://doi.org/10.3389/fpls.2017.00179

Alberti G, Candido P, Peressotti A, Turco S, Piussi P, Zerbi G (2005) Aboveground biomass relationships for mixed ash (*Fraxinus excelsior* L. and *Ulmus glabra* Hudson) stands in Eastern Prealps of Friuli Venezia Giulia (Italy). Annals of Forest Science 62(8): 831–836. https://doi.org/10.1051/forest:2005089

Ammer C (1996) Impact of ungulates on structure and dynamics of natural regeneration of mixed mountain forests in the Bavarian Alps. Forest Ecology and Management 88(1–2): 43–53. https://doi.org/10.1016/S0378-1127(96)03808-X

Baker M, King R, Kahle D (2023) TITAN2: Threshold Indicator Taxa Analysis. R package version 2.4.3. https://CRAN.R-project.org/package=TITAN2

Bakys R, Vasaitis R, Barklund P, Ihrmark K, Stenlid J (2009) Investigations concerning the role of *Chalara fraxinea* in declining *Fraxinus excelsior*. Plant Pathology 58(2): 284–292. https://doi.org/10.1111/j.1365-3059.2008.01977.x

Baraloto C, Goldberg DE, Bonal D (2005) Performance trade-offs among tropical tree seedlings in contrasting microhabitats. Ecology 86(9): 2461–2472. https://doi.org/10.1890/04-1956

Bartlow A, Lichti N, Curtis R, Swihart R, Steele M (2018) Re-caching of acorns by rodents: Cache management in eastern deciduous forests of North America. Acta Oecologica 92: 117–122. https://doi.org/10.1016/j.actao.2018.08.011

Bartoń K (2017) MuMIn: Multi-Model Inference. https://cran.r-project.org/web/packages/MuMIn/index.html

Batavia C, Nelson MP (2016) Conceptual ambiguities and practical challenges of ecological forestry: A critical review. Journal of Forestry 114(5): 572–581. https://doi.org/10.5849/jof.15-103

BDL (2024) Bank Danych o Lasach. https://www.bdl.lasy.gov.pl/portal/mapy-en [accessed 06 August 2024]

Blackburn TM, Pyšek P, Bacher S, Carlton JT, Duncan RP, Jarošík V, Wilson JRU, Richardson DM (2011) A proposed unified framework for biological invasions. Trends in Ecology & Evolution 26(7): 333–339. https://doi.org/10.1016/j.tree.2011.03.023

Borkowski J, Dobrowolska D, Dąbrowski W, Banul R, Załuski D (2017) Young conifer stands form a deer browsing refuge for an oak admixture: Silvicultural implications for forest regeneration under herbivore pressure. European Journal of Forest Research 136(5–6): 787–800. https://doi.org/10.1007/s10342-017-1070-3

Boucher D, Gauthier S, Thiffault N, Marchand W, Girardin M, Urli M (2020) How climate change might affect tree regeneration following fire at northern latitudes: A review. New Forests 51(4): 543–571. https://doi.org/10.1007/s11056-019-09745-6

Bouteiller XP, Bussolo M, Ségura R, Mariette S, Porté AJ (2023) Considering both sexual and clonal reproduction could help loosen the conflict of use over *Robinia pseudoacacia.* Dendrobiology 90: 30–38. https://doi.org/10.12657/denbio.090.002

Brooks ME, Kristensen K, van Benthem KJ, Magnusson A, Berg CW, Nielsen A, Skaug HJ, Maechler M, Bolker BM (2017) glmmTMB balances speed and flexibility among packages for zero-inflated generalized linear mixed modeling. The R Journal 9(2): 378–400. https://doi.org/10.32614/RJ-2017-066

Brown JK (1976) Estimating shrub biomass from basal stem diameters. Canadian Journal of Forest Research 6(2): 153–158. https://doi.org/10.1139/x76-019

Bruinderink GWTAG, Hazebroek E (1996) Wild boar (*Sus scrofa scrofa* L.) rooting and forest regeneration on podzolic soils in the Netherlands. Forest Ecology and Management 88(1–2): 71–80. https://doi.org/10.1016/S0378-1127(96)03811-X

Bury S, Dyderski MK (2024a) In search of *per capita* effects of *Prunus serotina* Ehrh. invasion on temperate forest understory alpha diversity. Biologia 79(10): 3011–3025. https://doi.org/10.1007/s11756-024-01766-7

Bury S, Dyderski MK (2024b) No effect of invasive tree species on aboveground biomass increments of oaks and pines in temperate forests. Forest Ecosystems 11: 100201. https://doi.org/10.1016/j.fecs.2024.100201

Campagnaro T, Brundu G, Sitzia T (2018) Five major invasive alien tree species in European Union forest habitat types of the Alpine and Continental biogeographical regions. Journal for Nature Conservation 43: 227–238. https://doi.org/10.1016/j.jnc.2017.07.007

Canham CD, Murphy L (2017) The demography of tree species response to climate: Sapling and canopy tree survival. Ecosphere 8(2): e01701. https://doi.org/10.1002/ecs2.1701

Catford JA, Wilson JRU, Pyšek P, Hulme PE, Duncan RP (2022) Addressing context dependence in ecology. Trends in Ecology & Evolution 37(2): 158–170. https://doi.org/10.1016/j.tree.2021.09.007

Chabrerie O, Verheyen K, Saguez R, Decocq G (2008) Disentangling relationships between habitat conditions, disturbance history, plant diversity, and American black cherry (*Prunus serotina* Ehrh.) invasion in a European temperate forest: Invasion-disturbance-ecosystem interactions. Diversity & Distributions 14(2): 204–212. https://doi.org/10.1111/j.1472-4642.2007.00453.x

Chakraborty D, Móricz N, Rasztovits E, Dobor L, Schueler S (2021) Provisioning forest and conservation science with high-resolution maps of potential distribution of major European tree species under climate change. Annals of Forest Science 78(2): 26. https://doi.org/10.1007/s13595-021-01029-4

Chmura D (2004) Penetration and naturalisation of invasive alien plant species (neophytes) in woodlands of the Silesian Upland (Southern Poland). Nature Conservation 60: 3–11.

Cierjacks A, Kowarik I, Joshi J, Hempel S, Ristow M, Von Der Lippe M, Weber E (2013) Biological flora of the British isles: *Robinia pseudoacacia*. Journal of Ecology 101(6): 1623–1640. https://doi.org/10.1111/1365-2745.12162

Closset-Kopp D, Chabrerie O, Valentin B, Delachapelle H, Decocq G (2007) When Oskar meets Alice: Does a lack of trade-off in r/K-strategies make *Prunus serotina* a successful invader of European forests? Forest Ecology and Management 247(1–3): 120–130. https://doi.org/10.1016/j.foreco.2007.04.023

Closset-Kopp D, Saguez R, Decocq G (2011) Differential growth patterns and fitness may explain contrasted performances of the invasive *Prunus serotina* in its exotic range. Biological Invasions 13(6): 1341–1355. https://doi.org/10.1007/s10530-010-9893-6

Conradi T, Van Meerbeek K, Ordonez A, Svenning J (2020) Biogeographic historical legacies in the net primary productivity of Northern Hemisphere forests. Ecology Letters 23: 800–810. https://doi.org/10.1111/ele.13481

Corenblit D, Steiger J, Tabacchi E, González E, Planty-Tabacchi A-M (2014) Ecosystem engineers modulate exotic invasions in riparian plant communities by modifying hydrogeomorphic connectivity: Ecosystem engineers modulate exotic invasions. River Research and Applications 30(1): 45–59. https://doi.org/10.1002/rra.2618

Crooks JA (2002) Characterizing ecosystem-level consequences of biological invasions: The role of ecosystem engineers. Oikos 97(2): 153–166. https://doi.org/10.1034/j.1600-0706.2002.970201.x

Czortek P, Królak E, Borkowska L, Bielecka A (2023) Effects of surrounding landscape on the performance of *Solidago canadensis* L. and plant functional diversity on heavily invaded post-agricultural wastelands. Biological Invasions 25(8): 2477–2494. https://doi.org/10.1007/s10530-023-03050-2

Czortek P, Adamowski W, Kamionka-Kanclerska K, Karpińska O, Zalewski A, Dyderski MK (2024) Patterns of *Prunus cerasifera* early invasion stages into a temperate primeval forest. Biological Invasions 26(3): 633–647. https://doi.org/10.1007/s10530-023-03188-z

Deckers B, Verheyen K, Vanhellemont M, Maddens E, Muys B, Hermy M (2008) Impact of avian frugivores on dispersal and recruitment of the invasive *Prunus serotina* in an agricultural landscape. Biological Invasions 10(5): 717–727. https://doi.org/10.1007/s10530-007-9164-3

deGroot M, Schueler S, Sallmannshofer M, Virgillito C, Kovacs G, Cech T, Božič G, Damjanić R, Ogris N, Hoch G, Kavčič A, Koltay A, Lanšćak M, Vujnović Z, Lukić I, Nagy L, Agbaba S, Orlović S, Poljaković-Pajnik L, Stojnić S, Westergren M, Zlatković M, Steinkellner M, Szamosvari E, Lapin K (2022) Forest management, site characteristics and climate change affect multiple biotic threats in riparian forests. Forest Ecology and Management 508: 120041. https://doi.org/10.1016/j.foreco.2022.120041

Dyderski MK, Bury S (2024) Dataset for Invasive *Prunus serotina* vs. *Robinia pseudoacacia*: How does temperate forest natural regeneration respond to their quantity? Figshare https://doi.org/10.6084/m9.figshare.26809084

Dyderski MK, Jagodziński AM (2018) Drivers of invasive tree and shrub natural regeneration in temperate forests. Biological Invasions 20(9): 2363–2379. https://doi.org/10.1007/s10530-018-1706-3

Dyderski MK, Jagodziński AM (2019) Similar Impacts of Alien and Native Tree Species on Understory Light Availability in a Temperate Forest. Forests 10(11): 951. https://doi.org/10.3390/f10110951

Dyderski MK, Jagodziński AM (2020) Impact of Invasive Tree Species on Natural Regeneration Species Composition, Diversity, and Density. Forests 11(4): 456. https://doi.org/10.3390/f11040456

Dyderski MK, Jagodziński AM (2021a) How do invasive trees impact shrub layer diversity and productivity in temperate forests? Annals of Forest Science 78(1): 20. https://doi.org/10.1007/s13595-021-01033-8

Dyderski MK, Jagodziński AM (2021b) Impacts of invasive trees on alpha and beta diversity of temperate forest understories. Biological Invasions 23(1): 235–252. https://doi.org/10.1007/s10530-020-02367-6

Dyderski MK, Paź S, Frelich LE, Jagodziński AM (2018) How much does climate change threaten European forest tree species distributions? Global Change Biology 24(3): 1150–1163. https://doi.org/10.1111/gcb.13925

Dyderski MK, Paź-Dyderska S, Jagodziński AM, Puchałka R (2025) Shifts in native tree species distributions in Europe under climate change. Journal of Environmental Management 373: 123504. https://doi.org/10.1016/j.jenvman.2024.123504

Dylewski Ł, Kurek P, Wiatrowska B, Jerzak L, Tryjanowski P (2017) Man-made perching sites – electricity pylons accelerate fleshy-fruited plants succession in farmlands. Flora 231: 51–56. https://doi.org/10.1016/j.flora.2017.04.004

Elton CS (1958) The Ecology of Invasions by Animals and Plants. Springer US, Boston, MA. https://doi.org/10.1007/978-1-4899-7214-9

Engel M, Nyssen B, Desie E, Den Ouden J, Raats L, Hagemann U (2024) Managing Black Cherry (*Prunus serotina* Ehrh.) in European Forests: Insights from native and non-native ranges. Forest Ecology and Management 562: 121959. https://doi.org/10.1016/j.foreco.2024.121959

Enríquez-de-Salamanca Á (2022) Effects of climate change on forest regeneration in Central Spain. Atmosphere 13(7): 1143. https://doi.org/10.3390/atmos13071143

European Commission [Eds] (2023) Guidelines on closer-to-nature forest management. Publications Office, Luxembourg, 1 pp. https://doi.org/10.2779/898789

Felton A, Lindbladh M, Brunet J, Fritz Ö (2010) Replacing coniferous monocultures with mixed-species production stands: An assessment of the potential benefits for forest biodiversity in northern Europe. Forest Ecology and Management 260(6): 939–947. https://doi.org/10.1016/j.foreco.2010.06.011

Forrester DI, Tachauer IHH, Annighoefer P, Barbeito I, Pretzsch H, Ruiz-Peinado R, Stark H, Vacchiano G, Zlatanov T, Chakraborty T, Saha S, Sileshi GW (2017) Generalized biomass and leaf area allometric equations for European tree species incorporating stand structure, tree age and climate. Forest Ecology and Management 396: 160–175. https://doi.org/10.1016/j.foreco.2017.04.011

Fuentes-Ramírez A, Pauchard A, Cavieres LA, García RA (2011) Survival and growth of *Acacia dealbata* vs. native trees across an invasion front in south-central Chile. Forest Ecology and Management 261(6): 1003–1009. https://doi.org/10.1016/j.foreco.2010.12.018

García RA, Fuentes-Lillo E, Cavieres L, Cóbar-Carranza AJ, Davis KT, Naour M, Núñez MA, Maxwell BD, Lembrechts JJ, Pauchard A (2023) *Pinus contorta* Alters Microenvironmental Conditions and Reduces Plant Diversity in Patagonian Ecosystems. Diversity 15(3): 320. https://doi.org/10.3390/d15030320

Gentili F, Cardarelli M, Bogliani C (2019) Comparing Negative Impacts of *Prunus serotina*, *Quercus rubra* and *Robinia pseudoacacia* on Native Forest Ecosystems. Forests 10(10): 842. https://doi.org/10.3390/f10100842

Godefroid S, Phartyal SS, Weyembergh G, Koedam N (2005) Ecological factors controlling the abundance of non-native invasive black cherry (*Prunus serotina*) in deciduous forest understory in Belgium. Forest Ecology and Management 210(1–3): 91–105. https://doi.org/10.1016/j.foreco.2005.02.024

González-Moreno P, Diez JM, Ibáñez I, Font X, Vilà M (2014) Plant invasions are context-dependent:multiscale effects of climate, human activity and habitat. Diversity & Distributions 20(6): 720–731. https://doi.org/10.1111/ddi.12206

Halarewicz A (2011) The reasons underlying the invasion of forest communities by black cherry, *Prunus serotina* and its subsequent consequences. Lesne Prace Badawcze 72(3): 267–272. https://doi.org/10.2478/v10111-011-0026-5

Hanewinkel M, Cullmann DA, Schelhaas M-J, Nabuurs G-J, Zimmermann NE (2013) Climate change may cause severe loss in the economic value of European forest land. Nature Climate Change 3(3): 203–207. https://doi.org/10.1038/nclimate1687

Hartig F (2022) DHARMa: Residual Diagnostics for Hierarchical (Multi-Level / Mixed) Regression Models. R package version 0.4.6. https://CRAN.R-project.org/package=DHARMa

Hejda M (2012) What Is the Impact of *Impatiens parviflora* on Diversity and Composition of Herbal Layer Communities of Temperate Forests? PLoS ONE 7: e39571. https://doi.org/10.1371/journal.pone.0039571

Horodecki P, Nowiński M, Jagodziński AM (2019) Advantages of mixed tree stands in restoration of upper soil layers on postmining sites: A five-year leaf litter decomposition experiment. Land Degradation & Development 30(1): 3–13. https://doi.org/10.1002/ldr.3194

Howe HF, Smallwood J (1982) Ecology of Seed Dispersal. Annual Review of Ecology and Systematics 13(1): 201–228. https://doi.org/10.1146/annurev.es.13.110182.001221

Il'ichev YuN, Ignat'ev LA, Artymuk SY (2011) The effect of forest fires and clearing of fire-destroyed stands on pedoecological conditions of natural forest regeneration. Contemporary Problems of Ecology 4(6): 634–640. https://doi.org/10.1134/S1995425511060117

Iszkuło G, Nowak-Dyjeta K, Sękiewicz M (2013) Influence of initial light intensity and deer browsing on *Taxus baccata* saplings: A six years field study. Dendrobiology 71: 93–99. https://doi.org/10.12657/denbio.071.009

Jagodziński AM, Oleksyn J (2009) Ecological consequences of silviculture at variable stand densities. III. Stand stability, phytoclimate and biodiversity. Sylwan 153: 219–230.

Jagodziński A, Dyderski M, Gęsikiewicz K, Horodecki P (2018) Tree- and Stand-Level Biomass Estimation in a *Larix decidua* Mill. Chronosequence. Forests 9(10): 587. https://doi.org/10.3390/f9100587

Jagodziński AM, Dyderski MK, Gęsikiewicz K, Horodecki P (2019) Effects of stand features on aboveground biomass and biomass conversion and expansion factors based on a *Pinus sylvestris* L. chronosequence in Western Poland. European Journal of Forest Research 138(4): 673–683. https://doi.org/10.1007/s10342-019-01197-z

Jagodziński AM, Horodecki P, Jasińska AK, Maliński T, Pilarek Z, Woźniak K, Wrońska-Pilarek D, Zieliński J, Dyderski MK (2024) Invasive × *Sorbaronia fallax* nothosubsp. *mitschurinii* affects temperate Scots pine forest biodiversity and functioning. Forest Ecology and Management 568: 122147. https://doi.org/10.1016/j.foreco.2024.122147

Jaworski A, Karczmarek S, Pach M (2007) Hodowla lasu. Tom 2. Sposoby odnowienia lasu. PWRiL, Warszawa.

Jiang P, Chen Y, Cao Y (2017) C:N:P Stoichiometry and Carbon Storage in a Naturally-Regenerated Secondary Quercus variabilis Forest Age Sequence in the Qinling Mountains, China. Forests 8(8): 281. https://doi.org/10.3390/f8080281

Käber Y, Bigler C, HilleRisLambers J, Hobi M, Nagel TA, Aakala T, Blaschke M, Brang P, Brzeziecki B, Carrer M, Cateau E, Frank G, Fraver S, Idoate-Lacasia J, Holik J, Kucbel S, Leyman A, Meyer P, Motta R, Samonil P, Seebach L, Stillhard J, Svoboda M, Szwagrzyk J, Vandekerkhove K, Vostarek O, Zlatanov T, Bugmann H (2023) Sheltered or suppressed? Tree regeneration in unmanaged European forests. Journal of Ecology 111(10): 2281–2295. https://doi.org/10.1111/1365-2745.14181

Kerr G, Mackintosh H (2012) Long-Term Survival of Saplings during the Transformation to Continuous Cover. Forests 3(3): 787–798. https://doi.org/10.3390/f3030787

Kowarik I, Hiller A, Planchuelo G, Seitz B, Von Der Lippe M, Buchholz S (2019) Emerging Urban Forests: Opportunities for Promoting the Wild Side of the Urban Green Infrastructure. Sustainability 11(22): 6318. https://doi.org/10.3390/su11226318

Kurek P, Wiatrowska B, Piechnik Ł, Holeksa J (2024) Phenological gap in fruiting period and dispersal of seeds from alien fleshy-fruited plants by medium-sized carnivores in temperate forests of Central Europe. NeoBiota 93: 321–337. https://doi.org/10.3897/neobiota.93.128008

Langmaier M, Lapin K (2020) A Systematic Review of the Impact of Invasive Alien Plants on Forest Regeneration in European Temperate Forests. Frontiers in Plant Science 11: 524969. https://doi.org/10.3389/fpls.2020.524969

Lanta V, Liancourt P, Altman J, Černý T, Dvorský M, Fibich P, Götzenberger L, Hornych O, Miklín J, Petřík P, Pyšek P, Čížek L, Doležal J (2022) Determinants of invasion by single versus multiple plant species in temperate lowland forests. Biological Invasions 24(8): 2513–2528. https://doi.org/10.1007/s10530-022-02793-8

Lázaro-Lobo A, Lucardi RD, Ramirez-Reyes C, Ervin GN (2021) Region-wide assessment of fine-scale associations between invasive plants and forest regeneration. Forest Ecology and Management 483: 118930. https://doi.org/10.1016/j.foreco.2021.118930

Levine JM, Vilà M, Antonio CMD, Dukes JS, Grigulis K, Lavorel S (2003) Mechanisms underlying the impacts of exotic plant invasions. Proceedings. Biological Sciences 270(1517): 775–781. https://doi.org/10.1098/rspb.2003.2327

Li Y, Ye S, Bai W, Zhang G (2023) Species diversity patterns differ by life stages in a pine-oak mixed forest. Dendrobiology 88: 138–149. https://doi.org/10.12657/denbio.088.010

Li Z, Mao C, Wu Q, Peng Y, Wang J, Zhang B, Zhang S, Liang X, Yan W, Chen X (2024) Temporal variations in aboveground biomass, nutrient content, and ecological stoichiometry in young and middle-aged stands of chinese fir forests. Plants 13(13): 1877. https://doi.org/10.3390/plants13131877

Lockwood JL, Cassey P, Blackburn T (2005) The role of propagule pressure in explaining species invasions. Trends in Ecology & Evolution 20(5): 223–228. https://doi.org/10.1016/j.tree.2005.02.004

Lonsdale WM (1999) Global patterns of plant invasions and the concept of invasibility. Ecology 80(5): 1522–1536. https://doi.org/10.1890/0012-9658(1999)080[1522:GPOPIA]2.0.CO;2

López-Núñez FA, Heleno RH, Ribeiro S, Marchante H, Marchante E (2017) Four-trophic level food webs reveal the cascading impacts of an invasive plant targeted for biocontrol. 98. https://doi.org/10.1002/ecy.1701

Lüdecke D (2018) ggeffects: Tidy Data Frames of Marginal Effects from Regression Models. Journal of Open Source Software 3(26): 772. https://doi.org/10.21105/joss.00772

Lygis V, Bakys R, Gustiene A, Burokiene D, Matelis A, Vasaitis R (2014) Forest self-regeneration following clear-felling of dieback-affected *Fraxinus excelsior*: Focus on ash. European Journal of Forest Research 133(3): 501–510. https://doi.org/10.1007/s10342-014-0780-z

Madsen P, Larsen JB (1997) Natural regeneration of beech (*Fagus sylvatica* L.) with respect to canopy density, soil moisture and soil carbon content. Forest Ecology and Management 97(2): 95–105. https://doi.org/10.1016/S0378-1127(97)00091-1

Marcolin E, Marzano R, Vitali A, Garbarino M, Lingua E (2019) Post-Fire Management Impact on Natural Forest Regeneration through Altered Microsite Conditions. Forests 10(11): 1014. https://doi.org/10.3390/f10111014

Maringer J, Wohlgemuth T, Neff C, Pezzatti GB, Conedera M (2012) Post-fire spread of alien plant species in a mixed broad-leaved forest of the Insubric region. Flora - Morphology, Distribution. Flora 207(1): 19–29. https://doi.org/10.1016/j.flora.2011.07.016

Maskell LC, Firbank LG, Thompson K, Bullock JM, Smart SM (2006) Interactions between non-native plant species and the floristic composition of common habitats. Journal of Ecology 94(6): 1052–1060. https://doi.org/10.1111/j.1365-2745.2006.01172.x

Medvecká J, Jarolímek I, Hegedüšová K, Škodová I, Bazalová D, Botková K, Šibíková M (2018) Forest habitat invasions – Who with whom, where and why. Forest Ecology and Management 409: 468–478. https://doi.org/10.1016/j.foreco.2017.08.038

Minotta G, Pinzauti S (1996) Effects of light and soil fertility on growth, leaf chlorophyll content and nutrient use efficiency of beech (*Fagus sylvatica* L.) seedlings. Forest Ecology and Management 86(1–3): 61–71. https://doi.org/10.1016/S0378-1127(96)03796-6

Modrý M, Hubený D, Rejšek K (2004) Differential response of naturally regenerated European shade tolerant tree species to soil type and light availability. Forest Ecology and Management 188(1–3): 185–195. https://doi.org/10.1016/j.foreco.2003.07.029

Mölder A, Sennhenn-Reulen H, Fischer C, Rumpf H, Schönfelder E, Stockmann J, Nagel R-V (2019) Success factors for high-quality oak forest (*Quercus robur*, *Q. petraea*) regeneration. Forest Ecosystems 6(1): 49. https://doi.org/10.1186/s40663-019-0206-y

Mousavi KSA, Ali Roshani G, Jalali SG, Shahrdami A (2012) The effects of cover crown, percentage and slope aspect on the quantitative distribution of the alder's saplings in forests of North of Iran. Resources and Environment 2: 17–20. https://doi.org/10.5923/j.re.20120201.02

Namura-Ochalska A, Borowa B (2015) Walka z czeremchą amerykańską *Padus serotina* (Ehrh.) Borkh. w leśnictwie Rózin w Kampinoskim Parku Narodowym; ocena skuteczności wybranych metod. In: Krzysztofiak L, Krzysztofiak A (Eds) Inwazyjne gatunki obcego pochodzenia zagrożeniem dla rodzimej przyrody red. Stowarzyszenie "Człowiek i Przyroda," Krzywe, 127–142.

Nyland RD (2007) Silviculture. Concepts and Applications. Waveland Press, Illinois.

Nyssen B, Vanhellemont M (2016) 5.6 Integrating black cherry in forest management in the Netherlands and Belgium. In: Krumm F, Vítková L (Eds) Introduced tree species in European forests: opportunities and challenges. European Forest Institute, 362–372.

Nyssen B, Ouden JD, Bindewald A, Brancalion P, Kremer K, Lapin K, Raats L, Schatzdorfer E, Stanturf J, Verheyen K, Muys B (2024) Established Invasive Tree Species Offer Opportunities for Forest Resilience to Climate Change. Current Forestry Reports 10(6): 456–486. https://doi.org/10.1007/s40725-024-00232-6

Oksanen J, Blanchet F, Kindt R (2018) vegan 2.3.3. Community Ecology Package. http://CRAN.R-project.org/package=vegan

Oliver CD, Larson BA (1996) Forest Stand Dynamics, Update Edition. Yale School of the Environment Other Publications 1. https://elischolar.library.yale.edu/fes_pubs/1

Oluwajuwon TV, Chazdon RL, Ota L, Gregorio N, Herbohn J (2024) Bibliometric and literature synthesis on assisted natural regeneration: an evidence base for forest and landscape restoration in the tropics. Frontiers in Forests and Global Change 7: 1412075. https://doi.org/10.3389/ffgc.2024.1412075

Palik BJ, D'Amato AW (2017) Ecological forestry: Much more than retention harvesting. Journal of Forestry 115(1): 51–53. https://doi.org/10.5849/jof.16-057

Petrášová M, Jarolímek I, Medvecká J (2013) Neophytes in Pannonian hardwood floodplain forests – History, present situation and trends. Forest Ecology and Management 308: 31–39. https://doi.org/10.1016/j.foreco.2013.07.041

Picchio R, Mederski PS, Tavankar F (2020) How and How Much, Do Harvesting Activities Affect Forest Soil, Regeneration and Stands? Current Forestry Reports 6(2): 115–128. https://doi.org/10.1007/s40725-020-00113-8

Puchałka R, Dyderski MK, Vítková M, Sádlo J, Klisz M, Netsvetov M, Prokopuk Y, Matisons R, Mionskowski M, Wojda T, Koprowski M, Jagodzinski AM (2021) Black locust (*Robinia pseudoacacia* L.) range contraction and expansion in Europe under changing climate. Global Change Biology 27(8): 1587–1600. https://doi.org/10.1111/gcb.15486

Puchałka R, Paź-Dyderska S, Jagodziński AM, Sádlo J, Vítková M, Klisz M, Koniakin S, Prokopuk Y, Netsvetov M, Nicolescu V-N, Zlatanov T, Mionskowski M, Dyderski MK (2023) Predicted range shifts of alien tree species in Europe. Agricultural and Forest Meteorology 341: 109650. https://doi.org/10.1016/j.agrformet.2023.109650

R Core Team (2023) R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna.

Radtke A, Ambraß S, Zerbe S, Tonon G, Fontana V, Ammer C (2013) Traditional coppice forest management drives the invasion of *Ailanthus altissima* and *Robinia pseudoacacia* into deciduous forests. Forest Ecology and Management 291: 308–317. https://doi.org/10.1016/j.foreco.2012.11.022

Rahmonov O (2009) The chemical composition of plant litter of black locust (*Robinia pseudoacacia* L.) and its ecological role in sandy ecosystems. Shengtai Xuebao. Acta Ecologica Sinica 29(4): 237–243. https://doi.org/10.1016/j.chnaes.2009.08.006

Rice SK, Westerman B, Federici R (2004) Impacts of the exotic, nitrogen-fixing black locust (*Robinia pseudoacacia*) on nitrogen- cycling in a pine-oak ecosystem. Plant Ecology 174(1): 97–107. https://doi.org/10.1023/B:VEGE.0000046049.21900.5a

Sádlo J, Vítková M, Pergl J, Pyšek P (2017) Towards site-specific management of invasive alien trees based on the assessment of their impacts: The case of *Robinia pseudoacacia.* NeoBiota 35: 1–34. https://doi.org/10.3897/neobiota.35.11909

Sapsford SJ, Brandt AJ, Davis KT, Peralta G, Dickie IA, Gibson RD, Green JL, Hulme PE, Nuñez MA, Orwin KH, Pauchard A, Wardle DA, Peltzer DA (2020) Towards a framework for understanding the context dependence of impacts of non-native tree species. Functional Ecology 34: 944–955. https://doi.org/10.1111/1365-2435.13544

Schmitt M (2020) Invasive Species and the Empty Niche Hypothesis – an essay. Mitteilungen der Deutschen Gesellschaft fur Allgemeine und Angewandte Entomologie, 235–239.

Simberloff D, Holle BV (1999) Positive Interactions of Nonindigenous Species: Invasional Meltdown? Biological Invasions 1(1): 21–32. https://doi.org/10.1023/A:1010086329619

Slabejová D, Čejka T, Hegedüšová K, Májeková J, Medvecká J, Mikulová K, Šibíková M, Škodová I, Šustek Z, Jarolímek I (2023) Comparison of alien *Robinia pseudoacacia* stands with native forest stands across different taxonomic groups. Forest Ecology and Management 548: 121413. https://doi.org/10.1016/j.foreco.2023.121413

Slowikowski K (2024) ggrepel: Automatically Position Non-Overlapping Text Labels with 'ggplot2. R package version 0.9.5. https://CRAN.R-project.org/package=ggrepel

Starfinger U, Kowarik I, Rode M, Schepker H (2003) From desirable ornamental plant to pest to accepted addition to the flora? – the perception of an alien tree species through the centuries. Biological Invasions 5(4): 323–335. https://doi.org/10.1023/B:BINV.0000005573.14800.07

Stohlgren TJ, Jarnevich C, Chong GW, Evangelista PH (2006) Scale and plant invasions: A theory of biotic acceptance. Preslia 78: 405–426.

Szwagrzyk J, Maciejewski Z, Maciejewska E, Tomski A, Gazda A (2018) Forest recovery in set-aside windthrow is facilitated by fast growth of advance regeneration. Annals of Forest Science 75(3): 80. https://doi.org/10.1007/s13595-018-0765-z

Szwagrzyk J, Gazda A, Muter E, Pielech R, Szewczyk J, Zięba A, Zwijacz-Kozica T, Wiertelorz A, Pachowicz T, Bodziarczyk J (2020) Effects of species and environmental factors on browsing frequency of young trees in mountain forests affected by natural disturbances. Forest Ecology and Management 474: 118364. https://doi.org/10.1016/j.foreco.2020.118364

Tavankar F, Bonyad AE, Nikooy M, Picchio R, Venanzi R, Calienno L (2017) Damages to soil and tree species by cable-skidding in Caspian forests of Iran. Forest Systems 26(1): e009. https://doi.org/10.5424/fs/2017261-09100

Terwei A, Zerbe S, Zeileis A, Annighöfer P, Kawaletz H, Mölder I, Ammer C (2013) Which are the factors controlling tree seedling establishment in North Italian floodplain forests invaded by non-native tree species? Forest Ecology and Management 304: 192–203. https://doi.org/10.1016/j.foreco.2013.05.003

Tinya F, Márialigeti S, Bidló A, Ódor P (2019) Environmental drivers of the forest regeneration in temperate mixed forests. Forest Ecology and Management 433: 720–728. https://doi.org/10.1016/j.foreco.2018.11.051

Turczański K, Dyderski MK, Rutkowski P (2021) Ash dieback, soil and deer browsing influence natural regeneration of European ash (*Fraxinus excelsior* L.). The Science of the Total Environment 752: 141787. https://doi.org/10.1016/j.scitotenv.2020.141787

Vanhellemont M, Verheyen K, De Keersmaeker L, Vandekerkhove K, Hermy M (2009) Does *Prunus serotina* act as an aggressive invader in areas with a low propagule pressure? Biological Invasions 11(6): 1451–1462. https://doi.org/10.1007/s10530-008-9353-8

Vítková M, Müllerová J, Sádlo J, Pergl J, Pyšek P (2017) Black locust (*Robinia pseudoacacia*) beloved and despised: A story of an invasive tree in Central Europe. Forest Ecology and Management 384: 287–302. https://doi.org/10.1016/j.foreco.2016.10.057

Wagner V, Chytrý M, Jiménez-Alfaro B, Pergl J, Hennekens S, Biurrun I, Knollová I, Berg C, Vassilev K, Rodwell JS, Škvorc Ž, Jandt U, Ewald J, Jansen F, Tsiripidis I, Botta-Dukát Z, Casella L, Attorre F, Rašomavičius V, Ćušterevska R, Schaminée JHJ, Brunet J, Lenoir J, Svenning J, Kącki Z, Petrášová-Šibíková M, Šilc U, García-Mijangos I, Campos JA, Fernández-González F, Wohlgemuth T, Onyshchenko V, Pyšek P (2017) Alien plant invasions in European woodlands. Diversity and Distributions 23: 969–981. https://doi.org/10.1111/ddi.12592

Wessely J, Essl F, Fiedler K, Gattringer A, Hülber B, Ignateva O, Moser D, Rammer W, Dullinger S, Seidl R (2024) A climate-induced tree species bottleneck for forest management in Europe. Nature Ecology & Evolution 8(6): 1109–1117. https://doi.org/10.1038/s41559-024-02406-8

Wiatrowska B, Kurek P, Moroń D, Celary W, Chrzanowski A, Trzciński P, Piechnik Ł (2023) Linear scaling – negative effects of invasive *Spiraea tomentosa* (Rosaceae) on wetland plants and pollinator communities. NeoBiota 81: 63–90. https://doi.org/10.3897/neobiota.81.95849

Wickham H (2016) ggplot2: Elegant Graphics for Data Analysis. https://doi.org/10.1007/978-3-319-24277-4_9

Zasada M (2017) Raport końcowy z tematu badawczego "Ekologiczne, gospodarcze i urządzeniowe konsekwencje występowania wybranych gatunków drzew obcych w Polsce" realizowanego w latach 2013–2017 przez Samodzielną Pracownię Dendrometrii i Nauki o Produkcyjności Lasu na zlecenie Dyrekcji Generalnej Lasów Państwowych w Warszawie. SGGW, Warszawa.

Supplementary material 1

Supplementary information

Authors: Sebastian Bury, Marcin K. Dyderski

Data type: docx

Explanation note: This file contains supplementary details about natural regeneration species frequency, allometric models used to aboveground biomass calculaction, and detailed data supporting the analyses presented in the manuscript

Link: https://doi.org/10.3897/neobiota.97.135421.suppl1

Table S1. The mean diameter in breast height (DBH) for trees with DBH<5cm, calculated from 102 plots, n = number of trees.

Species	Mean	n	SD	Remarks
Acer campestre L.	2.11	82	1.39	
Acer negundo L.	1.94	24	1.32	
Acer pseudoplatanus L.	1.43	261	1.32	Applied also for *A. platanoides*
Amelanchier spicata K.Koch	0.95	11	0.47	
×*Sorbaronia fallax* nothosubsp. *mitschurinii (*A.K.Skvortsov & Maitul.) Stalažs	1.08	5	0.72	
Betula pendula Roth	1.54	314	1.38	
Betula pubescens Ehrh.	0.20	1	0.00	
Carpinus betulus L.	1.88	246	1.49	
Carya ovata (Mill.) K.Koch	2.40	1	0.00	
Cerasus avium L.	2.41	6	1.28	
Cornus sanguinea L.	1.42	6	1.10	
Corylus avellana L.	1.60	421	1.13	
Crataegus laevigata DC.	1.68	28	1.19	
Crataegus monogyna Jacq.	1.59	56	0.96	
Crataegus rhipidophylla Gand.	1.45	14	0.81	
Euonymus europaeus L.	0.94	11	0.99	
Fagus sylvatica L.	1.71	259	1.30	
Frangula alnus Mill.	0.76	556	0.67	
Fraxinus excelsior L.	1.99	6	1.91	Applied also for *Syringa vulgaris*
Larix decidua Mill.	0.70	1	0.00	
Lonicera periclymenum L.	0.30	6	0.15	Applied also for *L. xylosteum*
Picea abies (L.) H.Karst.	2.27	8	1.02	
Pinus sylvestris L.	2.97	57	1.32	
Populus tremula L.	4.75	1	0.00	
Prunus cerasifera Ehrh.	0.51	9	0.53	
Prunus domestica L.	1.02	18	0.10	Applied also for *P. persica* and *P. spinosa*
Prunus mahaleb L.	2.00	1	0.00	
Prunus padus L.	1.06	1205	0.88	
Prunus serotina Ehrh.	1.31	3696	1.18	
Pseudotsuga menziesii Mirb.	4.02	3	0.88	
Pyrus pyraster (L.) Burgsd.	4.50	1	0.00	Applied also for *Malus* spp.
Quercus petraea (Matt.) Liebl.	1.58	342	1.25	
Quercus robur L.	2.58	79	1.26	
Quercus rubra L.	3.60	1	0.00	
Rhamnus cathartica L.	3.35	2	0.92	
Ribes spicatum Robson	0.30	1	0.00	
Ribes uva-crispa L.	0.29	9	0.03	Applied also for *R. rubrum* and *Rosa canina*
Robinia pseudoacacia L.	1.83	1036	1.38	
Sambucus nigra L.	1.80	98	1.22	
Sambucus racemosa L.	0.98	4	0.31	
Sorbus aucuparia L.	1.74	880	1.29	
Tilia cordata Mill.	1.45	102	1.22	
Tilia platyphyllos Scop.	2.20	3	2.23	
Ulmus minor Mill.	1.96	47	1.20	Applied also for other *Ulmus* spp.

Table S2. List of all woody species present in study plots and allometric models used for foliage biomass estimation (**Table S3**).

Species	**Taxa group**
×*Sorbaronia fallax* nothosubsp. *mitschurinii (*A.K.Skvortsov & Maitul.) Stalažs	*Cornus*
Acer campestre L.	*Acer*
Acer negundo L.	*Acer*
Acer platanoides L.	*Acer*
Acer pseudoplatanus L.	*Acer*
Aesculus hippocastanum L.	Broadleaved
Alnus glutinosa L.	*Alnus*
Amelanchier spicata K.Koch	*Amelanchier*
Betula pendula Roth	*Betula*
Betula pubescens Ehrh.	*Betula*
Carpinus betulus L.	*Carpinus*
Carya ovata (Mill.) K.Koch	Broadleaved
Cerasus avium L.	*Prunus serotina, Prunus*
Cornus sanguinea L.	*Cornus sanguinea*
Corylus avellana L.	*Corylus avellana*
Crataegus laevigata DC.	*Prunus serotina*
Crataegus monogyna Jacq.	*Prunus serotina, Prunus*
Crataegus rhipidophylla Gand.	*Prunus serotina, Prunus*
Euonymus europaeus L.	*Cornus sanguinea*
Fagus sylvatica L.	*Fagus*
Frangula alnus Mill.	*Frangula alnus*
Fraxinus excelsior L.	*Fraxinus*
Larix decidua Mill.	*Larix*
Lonicera periclymenum L.	*Cornus sanguinea*
Lonicera xylosteum L.	*Cornus sanguinea*
Malus domestica Borkh.	*Prunus serotina*
Malus sylvestris (L.) Mill.	*Prunus serotina*
Picea abies (L.) H.Karst.	*Picea*
Pinus sylvestris L.	*Pinus*
Populus tremula L.	*Populus*
Prunus cerasifera Ehrh.	*Prunus serotina*
Prunus domestica L.	*Prunus serotina*
Prunus mahaleb L.	*Prunus serotina*
Prunus padus L.	*Prunus serotina, Prunus*
Prunus persica (L.) Batsch	*Prunus serotina*
Prunus serotina Ehrh.	*Prunus serotina, Prunus*
Prunus spinosa L.	*Prunus serotina*
Pseudotsuga menziesii Mirb.	*Picea*
Pyrus pyraster (L.) Burgsd.	*Prunus serotina*
Quercus cerris L.	*Quercus*
Quercus petraea (Matt.) Liebl.	*Quercus*
Quercus robur L.	*Quercus*
Quercus rubra L.	*Quercus*
Rhamnus cathartica L.	*Cornus sanguinea*
Ribes rubrum L.	*Ribes*
Ribes spicatum Robson	*Ribes*
Ribes uva-crispa L.	*Ribes*

Robinia pseudoacacia L.	*Robinia*
Rosa canina L.	*Cornus sanguinea*
Salix alba L.	Broadleaved
Sambucus nigra L.	*Sambucus nigra*
Sambucus racemosa L.	*Sambucus nigra*
Sorbus aucuparia L.	*Sorbus aucuparia*
Syringa vulgaris L.	*Cornus sanguinea*
Tilia cordata Mill.	Broadleaved
Tilia platyphyllos Scop.	Broadleaved
Ulmus glabra Huds.	*Ulmus*
Ulmus laevis Pall.	*Ulmus*
Ulmus minor Mill.	*Ulmus*

Table S3. Allometric equations determining the biomass of particular tree species recorded on the study plots. Equations adopted were established for habitat conditions similar to those of this study. Abbreviations: DBH – diameter at breast height; CF - correction factor to reverse transformation of log-log models. Biomass components: AB – total aboveground biomass (ABW+FL), ABW – aboveground woody biomass, FL – foliage biomass. Taxa group is referenced to particular species in **Table S2**.

Taxa group	Biomass component	Unit	Source	R^2	N	DBH min [cm]	DBH max [cm]	Formula	a	b	CF
Acer	ABW	kg	Forrester et al. 2017	0.941	231	0	25	ln(Y)=ln(a)+b*ln(D), CF	-2.31160	2.41860	1.01050
Acer	ABW	kg	Forrester et al. 2017	0.969	3521	25	88	ln(Y)=ln(a)+b*ln(D), CF	-2.16530	2.41430	1.04148
Acer	FL	kg	Forrester et al. 2017	0.789	70	0	88	ln(Y)=ln(a)+b*ln(D), CF	-4.06250	2.06620	1.00318
Alnus	ABW	kg	Forrester et al. 2017	0.982	231	0	28.3	ln(Y)=ln(a)+b*ln(D), CF	-2.29180	2.40280	0.97779
Alnus	FL	kg	Forrester et al. 2017	0.578	231	0	28.3	ln(Y)=ln(a)+b*ln(D), CF	-4.46950	1.76230	0.97465
Amelanchier	AB	g	Brown 1976	0.990	39	0.4	4.5	ln(y)=a+b*ln(X)	3.60700	2.88700	NA
Amelanchier	FL	g	Brown 1976	0.830	39	0.4	4.5	ln(y)=a+b*ln(X)	1.69100	2.11100	NA
Betula	ABW	kg	Forrester et al. 2017	0.988	449	0	38	ln(Y)=ln(a)+b*ln(D), CF	-2.21180	2.37710	1.00799
Betula	FL	kg	Forrester et al. 2017	0.903	231	0	38	ln(Y)=ln(a)+b*ln(D), CF	-4.13700	1.88610	1.16321
Broadleaved	ABW	kg	Forrester et al. 2017	0.969	3521	0	88	ln(Y)=ln(a)+b*ln(D), CF	-2.16530	2.41430	1.04148
Broadleaved	FL	kg	Forrester et al. 2017	0.847	1824	0	88	ln(Y)=ln(a)+b*ln(D), CF	-4.22860	1.86250	1.06365
Carpinus betulus	AB	kg	Jagodziński, unpbl.	0.965	38	0	20	Y=a*D^b	0.04670	2.67655	NA
Carpinus betulus	FL	kg	Jagodziński, unpbl.	0.875	38	0	20	Y=a*D^b	0.01996	1.95261	NA
Cornus sanguinea	AB	kg	Jagodziński, unpbl.	0.892	52	0	8	Y=a*D^b	1.29073	1.23701	NA
Cornus sanguinea	FL	kg	Jagodziński, unpbl.	0.734	52	0	8	Y=a*D^b	0.13820	1.12562	NA
Corylus avellana	AB	kg	Jagodziński, unpbl.	0.926	96	0	16	Y=a*D^b	0.65347	1.37869	NA
Corylus avellana	FL	kg	Jagodziński, unpbl.	0.668	96	0	16	Y=a*D^b	0.09715	0.92685	NA
Fagus	ABW	kg	Forrester et al. 2017	0.975	712	0	82	ln(Y)=ln(a)+b*ln(D), CF	-1.78430	2.38950	1.09215
Fagus	FL	kg	Forrester et al. 2017	0.883	330	0	73	ln(Y)=ln(a)+b*ln(D), CF	-4.48130	1.90730	1.08752
Frangula alnus	AB	kg	Jagodziński, unpbl.	0.852	74	0	87	Y=a*D^b	0.16494	1.72121	NA
Frangula alnus	FL	kg	Jagodziński, unpbl.	0.704	74	0	87	Y=a*D^b	0.03785	0.94933	NA
Fraxinus	ABW	kg	Forrester et al. 2017	0.946	330	0	40	ln(Y)=ln(a)+b*ln(D), CF	-2.54360	2.61840	0.94631
Fraxinus	FL	kg	Forrester et al. 2017	0.872	158	0	69	ln(Y)=ln(a)+b*ln(D), CF	-4.85020	2.40640	0.80923
Larix	AB	kg	Jagodziński et al. 2018	0.971	96	2	58	Y=a*D^b	0.13800	2.39070	NA
Larix	FL	kg	Jagodziński et al. 2018	0.767	96	2	58	Y=a*D^b	0.00460	2.10360	NA
Picea	ABW	kg	Forrester et al. 2017	0.970	668	0	77	ln(Y)=ln(a)+b*ln(D), CF	-2.04640	2.30480	1.03300
Picea	FL	kg	Forrester et al. 2017	0.906	1007	0	77	ln(Y)=ln(a)+b*ln(D), CF	-2.79570	1.86880	1.02003

Pinus	AB	kg	Jagodziński et al. 2019	0.976	549	0	65	Y=a*D^b	0.20760	2.21850	NA
Pinus	FL	kg	Jagodziński et al. 2019	0.841	549	0	65	Y=a*D^b	0.03020	1.74200	NA
Populus	ABW	kg	Forrester et al. 2017	0.991	218	0	45	ln(Y)=ln(a)+b*ln(D), CF	-2.25670	2.36070	1.04492
Populus	FL	kg	Forrester et al. 2017	0.910	165	0	45	ln(Y)=ln(a)+b*ln(D), CF	-4.14540	1.94800	1.01172
Prunus	ABW	kg	Forrester et al. 2017	0.987	99	0	50	ln(Y)=ln(a)+b*ln(D), CF	-1.09680	2.09200	1.02629
Prunus	FL	kg	Forrester et al. 2017	0.545	99	0	50	ln(Y)=ln(a)+b*ln(D), CF	-4.10580	1.32120	0.95641
Prunus serotina	AB	kg	Jagodziński, unpbl.	0.974	50	0	15	Y=a*D^b	0.84778	1.44607	NA
Prunus serotina	FL	kg	Jagodziński, unpbl.	0.937	50	0	15	Y=a*D^b	0.04973	1.86895	NA
Quercus	ABW	kg	Forrester et al. 2017	0.990	579	0	77	ln(Y)=ln(a)+b*ln(D), CF	-2.31490	2.51330	1.03670
Quercus	FL	kg	Forrester et al. 2017	0.911	99	0	68	ln(Y)=ln(a)+b*ln(D), CF	-4.46630	2.13750	0.96633
Ribes	AB	g	Brown 1976	0.900	37	0.4	1.4	ln(y)=a+b*ln(X)	3.89200	3.12200	NA
Ribes	FL	g	Brown 1976	0.630	37	0.4	1.4	ln(y)=a+b*ln(X)	2.16400	2.53800	NA
Robinia	AB	kg	Zasada 2017	NA	22	7	46	Y=a*D^b	0.00030	2.51800	NA
Robinia	ABW	kg	Forrester et al. 2017	0.923	165	0	24	ln(Y)=ln(a)+b*ln(D), CF	-2.53440	2.45980	1.02110
Robinia	FL	kg	Forrester et al. 2017	0.936	99	0	24	ln(Y)=ln(a)+b*ln(D), CF	-2.79850	1.12780	1.02069
Robinia	FL	kg	Zasada 2017	NA	22	7	46	Y=a*D^b	0.00150	1.52880	NA
Sambucus nigra	AB	kg	Jagodziński, unpbl.	0.634	60	0	10	Y=a*D^b	1.34743	1.06650	NA
Sambucus nigra	FL	kg	Jagodziński, unpbl.	0.479	60	0	10	Y=a*D^b	0.18051	0.79876	NA
Sorbus aucuparia	AB	kg	Jagodziński, unpbl.	0.929	64	0	9	Y=a*D^b	0.15992	2.16383	NA
Sorbus aucuparia	FL	kg	Jagodziński, unpbl.	0.792	64	0	9	Y=a*D^b	0.02302	1.66533	NA
Ulmus	ABW	kg	Forrester et al. 2017	0.847	1824	0	88	ln(Y)=ln(a)+b*ln(D), CF	-4.22860	1.86250	1.06365
Ulmus	ABW	kg	Alberti et al. 2005	0.970	10	0	31	Y=a*D^b	0.10000	2.56000	NA
Ulmus	FL	kg	Forrester et al. 2017	0.969	3521	0	88	ln(Y)=ln(a)+b*ln(D), CF	-2.16530	2.41430	1.04148
Ulmus	FL	kg	Alberti et al. 2005	0.980	10	0	31	Y=a*D^b	0.13000	1.12000	NA

Table S4. List of species observed in the natural regeneration with their frequency [%]. Values above 20% were bolded (species assessed in the study).

Species	***P. serotina* poor**	***P. serotina* rich**	***R. pseudoacacia* poor**	***R. pseudoacacia* rich**
Acer campestre L.	0.0	6.3	3.1	**22.9**
Acer negundo L.*	0.0	0.0	0.0	4.2

Acer platanoides L.	10.4	**20.8**	11.1	**35.4**
Acer pseudoplatanus L.	10.4	**56.3**	11.1	**52.1**
Aesculus hippocastanum L.*	0.0	0.0	0.0	4.2
Alnus glutinosa L.	0.0	0.0	0.0	2.1
Amelanchier spicata K.Koch*	4.2	0.0	5.1	0.0
Betula pendula Roth	**47.9**	0.0	17.1	0.0
Carpinus betulus L.	6.3	**35.4**	7.1	**43.8**
Cerasus avium L.	6.3	10.4	7.1	**20.8**
Cornus sanguinea L.	0.0	2.1	0.0	2.1
Corylus avellana L.	4.2	12.5	3.1	**31.3**
Cotoneaster integerrimus Medik	0.0	0.0	0.0	2.1
Crataegus laevigata DC.	0.0	4.2	3.1	6.3
Crataegus monogyna Jacq.	0.0	14.6	3.1	8.3
Crataegus rhipidophylla Gand.	4.2	**25.0**	3.1	**20.8**
Euonymus europaeus L.	0.0	14.6	4.1	**25.0**
Fagus sylvatica L.	**29.2**	**52.1**	8.1	**25.0**
Frangula alnus Mill.	**66.7**	**20.8**	**31.1**	**20.8**
Fraxinus excelsior L.	0.0	**43.8**	6.1	**45.8**
Larix decidua Mill.	8.3	0.0	3.1	0.0
Lonicera xylosteum L.	0.0	2.1	3.1	0.0
Malus domestica Borkh.	0.0	0.0	3.1	2.1
Malus sylvestris (L.) Mill.	2.1	2.1	0.0	0.0
Picea abies (L.) H.Karst.	4.2	0.0	4.1	0.0
Pinus sylvestris L.	**35.4**	0.0	12.1	0.0
Populus tremula L.	0.0	0.0	0.0	2.1
Prunus cerasifera Ehrh.*	2.1	**22.9**	7.1	**25.0**
Prunus domestica L.	8.3	8.3	6.1	6.3
Prunus mahaleb L.*	0.0	0.0	3.1	0.0
Prunus padus L.	2.1	**27.1**	11.1	**56.3**
Prunus persica (L.) Batsch*	0.0	0.0	3.1	0.0
Prunus serotina Ehrh.*	**93.8**	**83.3**	**40.1**	**66.7**
Prunus spinosa L.	0.0	0.0	0.0	2.1
Pseudotsuga menziesii Mirb.*	0.0	0.0	3.1	0.0
Pyrus pyraster (L.) Burgsd.	6.3	**20.8**	7.1	14.6

Quercus cerris L.*	2.1	2.1	0.0	0.0
Quercus petraea (Matt.) Liebl.	**95.8**	**72.9**	**43.1**	**47.9**
Quercus robur L.	**27.1**	**20.8**	8.1	**20.8**
Quercus rubra L.*	18.8	12.5	8.1	16.7
Rhamnus cathartica L.	0.0	2.1	0.0	4.2
Ribes rubrum L.	0.0	6.3	0.0	8.3
Ribes spicatum Robson	0.0	4.2	0.0	2.1
Ribes uva-crispa L.	2.1	14.6	9.1	12.5
Robinia pseudoacacia L.*	10.4	10.4	**32.1**	**56.3**
Rosa canina L.	0.0	8.3	5.1	6.3
Sambucus nigra L.	0.0	**33.3**	14.1	**50.0**
Sambucus racemosa L.	0.0	0.0	5.1	4.2
×*Sorbaronia fallax* nothosubsp. *mitschurinii (*A.K.Skvortsov & Maitul.) Stalažs*	4.2	0.0	4.1	0.0
Sorbus aucuparia L.	**77.1**	**27.1**	**38.1**	**20.8**
Sorbus intermedia (Ehrh.) Pers	4.2	0.0	0.0	0.0
Taxus baccata L.	0.0	2.1	0.0	0.0
Tilia cordata Mill.	0.0	8.3	0.0	16.7
Tilia platyphyllos Scop.	0.0	0.0	0.0	2.1
Ulmus glabra Huds.	0.0	2.1	0.0	2.1
Ulmus minor Mill.	4.2	**27.1**	10.1	**29.2**

*Non-native species

Table S5. Results of Threshold Indicator Taxa Analysis for *P. serotina* on nutrient-poor sites.

Species	ienv.cp	zenv.cp	freq	maxgrp	IndVal	zscore	5%	10%	50%	90%	95%	purity	reliability	z.median	filter
Acer platanoides	1.82	1.69	5	2	24.83	3.10	0.55	1.45	1.82	2.25	2.57	0.97	0.77	3.95	0
Acer pseudoplatanus	2.63	2.63	5	2	38.14	3.89	0.40	0.65	2.47	2.63	2.66	0.78	0.62	3.06	0
Betula pendula	1.47	1.47	23	1	43.64	1.69	0.00	0.46	1.49	2.56	2.70	0.75	0.62	2.40	0
Carpinus betulus	1.56	1.56	3	2	11.41	1.06	0.00	0.00	1.54	2.57	2.63	0.78	0.31	1.99	0
Cerasus avium	0.00	2.63	3	2	16.15	1.01	0.00	0.00	1.59	2.63	2.63	0.64	0.31	2.46	0
Fagus sylvatica	2.21	2.21	14	2	38.28	2.44	0.00	0.00	1.82	2.24	2.28	0.88	0.73	3.02	0

Frangula alnus	1.13	1.13	32	2	51.57	1.25	0.00	0.00	0.94	1.74	2.27	0.76	0.48	1.93	0
Larix decidua	1.47	1.47	4	1	14.29	1.43	0.00	0.00	1.28	1.49	1.54	0.56	0.30	1.81	0
Pinus sylvestris	1.47	1.47	17	1	48.29	3.02	0.00	0.00	0.80	1.49	1.52	0.97	0.91	3.53	0
Prunus domestica	0.00	0.84	4	1	11.18	0.72	0.00	0.00	0.84	2.17	2.21	0.60	0.24	1.69	0
Prunus serotina	0.08	1.02	44	2	90.85	3.31	0.00	0.00	0.74	1.43	1.91	1.00	1.00	3.86	2
Pyrus pyrraster	0.84	0.84	3	2	12.00	1.52	0.66	0.76	1.56	2.24	2.25	0.91	0.32	2.06	0
Quercus petraea	0.00	1.59	45	1	70.33	3.47	0.00	0.00	1.49	1.77	2.21	0.97	0.94	3.50	0
Quercus robur	0.00	0	13	2	32.50	0.95	0.00	0.00	0.23	1.59	1.67	0.52	0.31	-1.64	0
Quercus rubra	0.08	0.08	8	1	19.09	0.92	0.00	0.00	0.00	2.24	2.25	0.73	0.62	2.48	0
Robinia pseudoacacia	0.00	0.00	4	1	16.15	0.74	0.00	0.00	0.66	2.23	2.30	0.52	0.41	2.49	0
Sorbus aucuparia	0.00	0.00	36	2	72.73	3.32	0.00	0.00	1.31	1.74	2.25	0.96	0.81	3.15	0

ienv.cp ─ environmental change point for each taxon based on IndVal maximum; **zenv.cp** ─ environmental change point for each taxon based on z maximum; **freq** ─ number of non-zero abundance values per taxon; **maxgrp** ─ 1 if z- (negative response); 2 if z+ (positive response); **IndVal** ─ Dufrene and Legendre 1997 IndVal statistic, scaled 0-100%; **zscore** ─ IndVal *z* score; **5%, 10%, 50%, 90%, 95%** ─ change point quantiles among bootstrap replicates; **purity** ─ proportion of replicates matching observed **maxgrp** assignment; reliability ─ proportion of replicate obsiv.prob values < = 0.05; **z.median** ─ median score magnitude across all bootstrap replicates; **filter** ─ logical (if >0) indicating whether each taxa met purity and reliability criteria, value indicates maxgrp assignment. Abbreviations from Baker et al. (2020).

Table S6. Results of Threshold Indicator Taxa Analysis for *P. serotina* on nutrient-rich sites.

Species	**ienv.cp**	**zenv.cp**	**freq**	**maxgrp**	**IndVal**	**zscore**	**5%**	**10%**	**50%**	**90%**	**95%**	**purity**	**reliability**	**z.median**	**filter**
Acer campestre	1.07	1.07	3	1	12.50	1.76	0.00	0.00	1.07	1.13	1.19	0.84	0.25	1.94	0
Acer platanoides	1.52	1.52	10	2	36.96	3.08	0.41	1.46	1.52	2.06	2.09	0.97	0.86	3.65	0
Acer pseudoplatanus	1.07	1.13	27	2	52.18	1.88	0.00	0.00	1.13	2.50	2.75	0.69	0.63	2.27	0
Carpinus betulus	1.46	1.46	17	1	46.31	1.77	0.00	0.00	1.19	1.88	1.92	0.76	0.68	2.35	0
Cerasus avium	0.00	0.00	5	1	21.32	1.72	0.00	0.00	1.00	2.72	2.82	0.59	0.48	2.35	0
Corylus avellana	0.00	1.13	6	2	13.69	0.63	0.00	0.00	1.30	2.82	3.00	0.59	0.34	1.79	0
Crataegus monogyna	2.50	1.19	7	1	14.27	0.43	0.00	0.00	1.18	2.15	2.24	0.51	0.35	1.84	0
Crataegus rhipidophylla	2.00	2.00	12	1	25.79	0.68	0.00	0.00	1.28	2.00	2.07	0.59	0.46	1.99	0
Euonymus europaeus	2.72	1.90	7	2	25.29	2.49	0.00	1.07	2.01	2.82	2.82	0.91	0.75	3.57	0
Fagus sylvatica	2.72	2.72	25	2	46.49	0.61	0.00	0.00	1.00	2.72	2.79	0.63	0.49	1.95	0
Frangula alnus	1.70	1.70	10	2	26.11	1.61	0.00	0.09	1.46	2.20	2.82	0.81	0.56	2.18	0
Fraxinus excelsior	1.83	1.83	21	2	47.33	1.89	0.00	0.00	1.83	2.46	2.50	0.74	0.62	2.31	0
Prunus cerasifera	1.97	1.94	11	2	34.25	2.93	0.00	0.00	1.97	2.09	2.12	0.86	0.77	3.23	0
Prunus domestica	2.72	2.72	4	2	16.75	0.99	0.00	0.00	1.51	2.82	2.82	0.61	0.36	1.94	0
Prunus padus	1.97	1.83	13	2	42.37	3.72	0.09	1.32	1.95	2.09	2.12	0.94	0.90	4.25	0

Prunus serotina	2.72	1.13	40	2	82.46	3.37	0.00	0.00	0.52	2.16	2.24	1.00	1.00	4.00	2
Pyrus pyrraster	0.00	1.94	10	2	21.74	0.65	0.00	0.00	1.33	1.95	2.28	0.73	0.42	1.89	0
Quercus petraea	1.70	1.70	35	1	80.06	3.60	0.47	0.76	1.54	1.70	1.75	0.99	0.99	3.72	1
Quercus robur	2.72	2.72	10	2	77.91	8.21	1.55	1.60	2.54	2.93	3.00	0.99	0.94	6.04	0
Quercus rubra	2.72	1.19	6	2	20.95	2.25	0.83	1.12	1.83	2.72	2.72	0.93	0.70	3.42	0
Ribes rubrum	1.42	1.42	3	2	15.00	2.48	0.74	1.24	1.42	1.86	1.95	0.94	0.44	2.49	0
Ribes uva-crispa	0.36	0.36	7	2	24.14	2.24	0.17	0.26	1.13	1.86	1.94	0.86	0.67	2.58	0
Robinia pseudoacacia	0.00	0.00	5	2	14.29	0.72	0.00	0.00	1.07	2.24	2.75	0.62	0.31	1.70	0
Rosa canina	0.00	0.00	4	2	10.53	0.21	0.00	0.00	0.35	2.12	2.20	0.38	0.25	1.72	0
Sambucus nigra	0.00	1.90	16	1	29.77	0.65	0.00	0.00	0.70	1.90	1.93	0.60	0.46	1.94	0
Sorbus aucuparia	2.00	2.00	13	1	34.21	1.84	0.00	0.09	1.99	2.07	2.11	0.82	0.50	2.11	0
Tilia cordata	2.00	2.00	4	2	17.67	1.68	0.00	0.00	1.69	2.00	2.07	0.80	0.42	2.13	0
Ulmus minor	0.00	0.00	13	2	30.39	1.38	0.00	0.00	0.42	2.09	2.09	0.69	0.50	2.03	0

Abbreviations: see **Table S5**.

Table S7. Results of Threshold Indicator Taxa Analysis for *R. pseudoacacia* on nutrient-poor sites.

Species	ienv.cp	zenv.cp	freq	maxgrp	IndVal	zscore	5%	10%	50%	90%	95%	purity	reliability	z.median	filter
Acer platanoides	1.06	1.34	9	2	33.28	3.01	1.01	1.05	1.34	3.35	3 .42	0.99	0.94	3.56	0
Acer pseudoplatanus	1.34	1.34	9	2	28.06	1.87	0.30	0.40	1.96	3.14	3 .16	0.94	0.68	2.60	0
Amelanchier spicata	3.48	0.74	3	2	10.00	0.76	0.38	0.74	2.17	3.55	3 .62	0.76	0.26	1.72	0
Betula pendula	2.06	2.17	15	1	43.39	3.47	0.00	0.00	2.06	2.17	2 .38	1.00	0.98	4.49	1
Carpinus betulus	3.23	3.23	5	2	18.89	1.07	0.00	1.02	2.06	3.30	3 .68	0.75	0.40	2.30	0
Cerasus avium	1.72	1.72	5	2	16.05	1.53	0.00	0.29	1.72	2.93	3 .21	0.80	0.41	1.97	0
Fagus sylvatica	0.00	0.00	6	1	14.92	0.67	0.00	0.00	0.00	2.56	3 .04	0.72	0.46	2.12	0
Frangula alnus	3.48	2.56	29	2	41.40	0.43	0.00	0.00	1.02	3.49	3 .62	0.50	0.43	1.83	0
Fraxinus excelsior	1.02	1.02	4	2	14.29	1.42	0.82	0.95	1.72	3.55	3 .81	0.79	0.34	1.98	0
Pinus sylvestris	0.00	1.02	10	1	50.00	5.60	0.00	0.00	0.30	1.06	1 .09	1.00	1.00	6.60	1
Prunus cerasifera	1.02	1.02	5	2	17.86	1.80	0.81	0.94	1.11	2.29	2 .73	0.87	0.45	2.17	0
Prunus domestica	2.74	2.74	4	1	11.43	0.51	0.00	0.00	0.94	2.56	2 .74	0.66	0.17	1.39	0
Prunus padus	2.17	2.38	9	2	36.26	3.70	1.02	1.68	2.20	2.93	2 .93	1.00	0.97	4.58	2
Prunus serotina	3.16	2.93	38	1	53.66	0.54	0.00	0.00	1.23	3.09	3 .16	0.56	0.50	1.94	0
Pyrus pyrraster	3.23	1.12	5	2	19.23	2.83	1.06	1.11	2.27	3.23	3 .62	0.99	0.74	3.62	0
Quercus petraea	1.34	1.34	41	1	86.67	5.99	1.17	1.33	1.72	2.06	2 .13	1.00	1.00	5.93	1

Quercus robur	0.00	0.00	6	1	19.43	1.12	0.00	0.00	0.74	3.18	3 .23	0.78	0.45	1.83	0
Quercus rubra	0.00	0.00	6	1	33.79	3.44	0.00	0.00	0.10	3.30	3 .35	0.83	0.70	3.29	0
Ribes uva crispa	2.24	2.17	7	2	22.34	1.81	0.00	0.86	2.24	2.56	3 .16	0.83	0.58	2.27	0
Robinia pseudoacacia	0.40	0.74	30	2	87.53	7.37	0.10	0.30	0.61	2.04	2 .09	1.00	1.00	8.19	2
Rosa canina	1.72	1.72	3	2	13.04	1.95	1.08	1.33	1.72	2.67	2 .77	0.89	0.29	2.08	0
Sambucus nigra	2.17	2.27	12	2	46.88	4.82	0.74	1.13	2.20	2.90	3 .17	1.00	0.99	5.55	2
Sambucus racemosa	1.16	1.16	3	2	12.00	1.37	0.00	1.06	1.16	2.30	2 .38	0.76	0.21	1.77	0
Sorbus aucuparia	1.16	1.12	36	2	49.75	0.87	0.00	0.00	1.16	3.48	3 .62	0.63	0.48	1.96	0
Ulmus minor	1.02	0.94	8	2	27.59	2.25	0.82	0.94	1.16	2.29	2 .38	0.97	0.84	3.21	0

Abbreviations: see **Table S5**.

Table S8. Results of Threshold Indicator Taxa Analysis for *R. pseudoacacia* on nutrient-rich sites.

Species	**ienv.cp**	**zenv.cp**	**freq**	**maxgrp**	**IndVal**	**zscore**	**5%**	**10%**	**50%**	**90%**	**95%**	**purity**	**reliability**	**z.median**	**filter**
Acer campestre	2.84	2.84	11	2	36.53	3.22	0.60	0.63	2.84	4.05	4.43	0.99	0.92	3.68	0
Acer platanoides	2.10	2.10	17	2	58.02	4.21	1.01	1.05	2.33	3.89	4.38	1.00	0.98	4.63	2
Acer pseudoplatanus	1.75	1.75	25	2	40.63	0.64	0.00	0.00	2.07	4.78	4.81	0.53	0.43	1.75	0
Carpinus betulus	0.00	0.00	21	1	60.15	2.98	0.00	0.00	0.30	3.92	4.29	0.63	0.63	2.30	0
Cerasus avium	2.02	2.02	10	1	30.48	1.70	0.00	0.00	1.80	2.31	2.73	0.79	0.57	2.10	0
Corylus avellana	3.92	3.92	15	2	51.39	4.10	0.82	0.97	3.70	4.81	4.95	0.99	0.94	5.00	0
Crataegus laevigata	0.00	0.00	3	1	15.35	1.07	0.00	0.00	1.08	4.38	4.38	0.55	0.33	2.00	0
Crataegus monogyna	3.53	3.53	4	1	11.43	0.54	0.00	0.00	1.05	3.33	3.53	0.59	0.26	1.67	0
Crataegus rhipidophylla	4.38	4.38	10	2	26.37	1.09	0.00	0.00	2.85	4.38	4.38	0.60	0.49	2.14	0
Euonymus europaeus	4.38	3.92	12	2	44.74	3.86	1.23	1.36	3.60	4.38	4.48	0.99	0.95	4.65	2
Fagus sylvatica	0.00	0.00	12	1	42.64	3.49	0.00	0.00	0.30	2.02	2.11	0.97	0.89	4.25	0
Frangula alnus	3.78	1.18	10	2	29.69	2.44	1.05	1.11	2.61	3.89	4.60	0.97	0.86	3.85	0
Fraxinus excelsior	4.70	3.41	22	2	47.82	1.97	0.63	0.97	3.41	4.30	4.70	0.82	0.68	2.55	0
Prunus cerasifera	3.78	3.78	12	2	26.49	0.79	0.00	0.00	2.73	3.89	4.05	0.70	0.50	1.96	0
Prunus domestica	0.00	4.38	3	2	11.37	0.41	0.00	0.00	0.98	4.38	4.38	0.46	0.33	2.16	0
Prunus padus	0.00	0.30	27	2	60.73	3.68	0.00	0.00	0.30	2.02	3.70	0.94	0.95	3.89	0
Prunus serotina	4.70	4.70	32	2	73.09	2.10	0.00	0.81	3.53	4.70	4.72	0.87	0.67	2.48	0
Pyrus pyrraster	3.53	3.53	7	1	20.00	1.19	0.00	0.00	2.10	3.59	3.63	0.71	0.31	1.75	0
Quercus petraea	0.00	0.00	23	1	84.38	5.05	0.00	0.00	0.89	1.11	1.50	1.00	1.00	5.16	1
Quercus robur	2.10	2.10	10	2	41.61	5.40	1.75	2.00	2.61	4.02	4.29	1.00	0.99	5.82	2
Quercus rubra	3.78	3.78	8	2	30.35	2.95	1.08	1.12	2.50	4.29	4.70	0.96	0.79	3.65	0

Ribes rubrum	1.01	1.01	4	2	14.81	1.20	0.91	1.01	2.02	4.63	4.81	0.86	0.46	2.15	0
Ribes uva crispa	0.75	0.75	6	2	20.00	1.66	0.48	0.66	1.01	2.44	4.33	0.63	0.50	2.28	0
Robinia pseudoacacia	0.30	0.30	27	2	76.10	6.04	0.00	0.00	0.42	3.53	3.63	1.00	1.00	6.20	2
Rosa canina	3.17	0.75	3	1	9.26	0.63	0.00	0.00	0.75	2.98	3.17	0.68	0.24	1.63	0
Sambucus nigra	0.00	0.00	24	2	50.45	1.75	0.00	0.00	0.75	3.41	3.70	0.67	0.54	2.08	0
Sorbus aucuparia	0.00	3.32	10	1	19.48	0.65	0.00	0.00	0.91	4.81	4.95	0.63	0.52	2.14	0
Tilia cordata	1.18	1.18	8	2	21.65	1.71	0.00	0.33	1.18	3.78	3.92	0.71	0.44	1.95	0
Ulmus minor	3.92	3.92	14	2	44.91	3.10	0.00	0.30	3.70	4.02	4.03	0.94	0.84	3.55	0

Abbreviations: see **Table S5**.

Table S9. The parameters of Generalized Linear Mixed-Effect Models for the impact of *P. serotina* aboveground biomass (AB) on saplings density on nutrient-poor sites. Abbreviation in parentheses for each species indicates the distribution of dependent variable.

Response	Variable	Estimate	SE	z	Pr(>|z|)
All alien species (P)	(Intercept)	3.4555	1.2942	2.670	0.008
obs. = 47	log1p(Biomass)	-0.9295	0.1012	-9.186	<0.001
AICc = 285.7	Age	-0.0437	0.0054	-8.074	<0.001
$AICc_0$ = 425.3					
Random effect SD:					
Year = 2.1149					
Forest District = 0.0000					
***Q. petraea* (NB)**	(Intercept)	3.7636	0.5829	6.457	<0.001
obs. = 47	log1p(Biomass)	-0.3164	0.1542	-2.051	0.040
AICc = 371.4	Age	-0.0095	0.0067	-1.417	0.157
$AICc_0$ = 371.8					
Random effect SD:					
Year = 3.749e-01					
Forest District = 7.249e-05					
***Q. robur* (P)**	(Intercept)	1.7231	2.2775	0.757	0.449
obs. = 47	log1p(Biomass)	-1.4210	0.1383	-10.273	<0.001
AICc = 210.4	Age	-0.0351	0.0077	-4.539	<0.001
$AICc_0$ = 369.2					
Random effect SD:					
Year = 3.3660					

Forest District = 0.4511					
***P. sylvestris* (P)**	(Intercept)	0.5171	1.2339	0.419	0.675
obs. = 47	log1p(Biomass)	-0.5056	0.0945	-5.348	<0.001
AICc = 696.9					
$AICc_0$ = 727.6					
Random effect SD:					
Year = 1.6828					
Forest District = 0.7432					
***P. serotina* (NB)**	(Intercept)	3.2640	0.6053	5.392	<0.001
obs. = 47	log1p(Biomass)	1.1704	0.1472	7.952	<0.001
AICc = 428.6	Age	-0.0160	0.0076	-2.102	0.036
$AICc_0$ = 460.4					
Random effect SD:					
Year = 0.0593					
Forest District = 0.0003					
***S. aucuparia* (P)**	(Intercept)	1.3118	0.7508	1.747	0.081
obs. = 47	log1p(Biomass)	0.0880	0.0436	2.018	0.044
AICc = 817.2	Age	0.0052	0.0021	2.474	0.013
$AICc_0$ = 823.8					
Random effect SD:					
Year = 1.2419					
Forest District = 0.0977					
***B. pendula* (P)**	(Intercept)	0.3850	0.8156	0.472	0.637
obs. = 47	log1p(Biomass)	0.3417	0.1126	3.035	0.002
AICc = 304.4	Age	-0.0096	0.0047	-2.044	0.041
$AICc_0$ = 316.0					
Random effect SD:					
Year = 1.149e+00					
Forest District = 3.705e-05					

Abbreviations: **SE** – standard error; **z** – z-test statistic; **Pr(>|z|)** – p-value; **AICc** – Akaike's Information Criterion; **$AICc_0$** – AICc of null model; **SD** – standard deviation; **P** – Poisson distribution; **NB** – negative binomial distribution

Table S10. The parameters of Generalized Linear Mixed-Effect Models for the impact of *P. serotina* aboveground biomass (AB) on saplings density on nutrient-rich sites. Abbreviation in parentheses for each species indicates the distribution of dependent variable.

Response	Variable	Estimate	SE	z	Pr(>|z|)
***Q. petraea* (P)**	(Intercept)	1.5967	2.0037	0.797	0.426
obs. = 48	log1p(Biomass)	-0.8586	0.0376	-22.809	<0.001
AICc = 4180.6	Age	-0.0039	0.0007	-5.382	<0.001
$AICc_0$ = 4889.0					
Random effect SD:					
Year = 2.2900					
Forest District = 3.0390					
***C. betulus* (P)**	(Intercept)	-1.0013	0.8468	-1.182	0.237
obs. = 47	log1p(Biomass)	-0.2557	0.1164	-2.196	0.028
AICc = 507.3	Age	0.0132	0.0027	4.835	<0.001
$AICc_0$ = 534.1					
Random effect SD:					
Year = 0.0002					
Forest District = 1.6188					
***P. serotina* (P)**	(Intercept)	0.3991	0.5934	0.673	0.501
obs. = 48	log1p(Biomass)	1.0705	0.0393	27.271	<0.001
AICc = 2210.7	Age	0.0057	0.0013	4.224	<0.001
$AICc_0$ = 3168.6					
Random effect SD:					
Year = 0.4050					
Forest District = 1.0840					
***F. excelsior* (ZI-P)**	(Intercept)	-1.5433	0.8758	-1.762	0.078
obs. = 48	log1p(Biomass)	0.8618	0.0672	12.819	<0.001
AICc = 495.0	Age	0.0285	0.0029	9.958	<0.001
$AICc_0$ = 743.7	Zero inflation(Intercept)	0.0270	0.3118	0.087	0.931
Random effect SD:					
Year = 3.406e-05					
Forest District = 1.774e+00					
Zero inflation Year = 7.117e-05					
Zero inflation F. Dist. = 9.330e-05					

***U. minor* (P)**	(Intercept)	-1.9200	1.0244	-1.874	0.061
obs. = 48	log1p(Biomass)	0.5837	0.1252	4.662	<0.001
AICc = 278.1					
$AICc_0$ = 298.1					
Random effect SD:					
Year = 0.0002					
Forest District = 1.9132					
***P. padus* (P)**	(Intercept)	-1.9200	1.0244	-1.874	0.061
obs. = 48	log1p(Biomass)	0.5837	0.1252	4.662	<0.001
AICc = 247.2					
$AICc_0$ = 325.0					
Random effect SD:					
Year = 0.8349					
Forest District = 1.8871					

Abbreviations: **SE** – standard error; **z** – z-test statistic; **Pr(>|z|)** – p-value; **AICc** – Akaike's Information Criterion; **$AICc_0$** – AICc of null model; **SD** – standard deviation; **P** – Poisson distribution; **ZI-P ─** zero-inflation Poisson distribution

Table S11. The parameters of Generalized Linear Mixed-Effect Models for the impact of *R. pseudoacacia* aboveground biomass (AB) on sapling density on nutrient-poor sites. Abbreviation in parentheses for each species indicates the distribution of dependent variable.

Response	Variable	Estimate	SE	z	Pr(>|z|)
All alien species (NB)	(Intercept)	1.1557	0.2792	4.139	<0.001
obs. = 48	log1p(Biomass)	0.3993	0.0850	4.696	<0.001
AICc = 274.0					
$AICc_0$ = 291.9					
Random effect SD:					
Year = 1.916e-05					
Forest District = 2.101e-05					
***Q. petraea* (P)**	(Intercept)	3.1890	0.5341	5.971	<0.001
obs. = 48	log1p(Biomass)	-0.5535	0.0396	-13.982	<0.001
AICc = 720.9	Age	-0.0088	0.0018	-4.888	<0.001
$AICc_0$ = 1042.4					

Random effect SD:					
Year = 0.6877					
Forest District = 0.6122					
***S. aucuparia* (ZI-P)**	(Intercept)	2.0475	0.3433	5.964	<0.001
obs. = 48	log1p(Biomass)	0.1134	0.0352	3.219	0.001
AICc = 497.0	Zero inflation:(Intercept)	-1.1802	0.4052	-2.913	0.004
$AICc_0$ = 507.3					
Random effect SD:					
Year = 6.589e-05					
Forest District = 7.304e-01					
Zero inflation: Year = 0.3114					
Zero inflation: F. Dist. = 0.0002					
***R. pseudoacacia* (ZI-P)**	(Intercept)	2.3151	0.3694	6.268	<0.001
obs. = 48	Zero inflation: (Intercept)	1.7454	0.6279	2.198	0.005
AICc = 347.5	Zero inflation: log1p(Biomass)	-2.1411	0.6099	-3.510	0.000
$AICc_0$ = 381.5					
Random effect SD:					
Year = 6.589e-05					
Forest District = 7.304e-01					
Zero inflation: Year = 6.495e-05					
Zero inflation: F. Dist. = 7.208e-05					

Abbreviations: **SE** – standard error; **z** – z-test statistic; **Pr(>|z|)** – p-value; **AICc** – Akaike's Information Criterion, **$AICc_0$** – AICc of null model; **SD** – standard deviation; **P** – Poisson distribution; **ZI-P ─** zero-inflation Poisson distribution; **NB ─** negative binomial distribution

Table S12. The parameters of Generalized Linear Mixed-Effect Models for the impact of *R. pseudoacacia* aboveground biomass (AB) on sapling density on nutrient-rich sites. Abbreviation in parentheses for each species indicates the distribution of dependent variable.

	Variable	Estimate	SE	z	Pr(>|z|)
All alien species (NB)	(Intercept)	1.0281	0.4010	2.564	0.010
obs. = 48	log1p(Biomass)	0.2878	0.0879	3.275	0.001
AICc = 261.1					
$AICc_0$ = 270.0					

Random effect SD:					
Year = 3.338e-01					
Forest District = 4.766e-05					
***Q. petraea* (P)**	(Intercept)	1.0680	0.8364	1.277	0.202
obs. = 48	log1p(Biomass)	-0.8439	0.0461	-18.300	<0.001
AICc = 1807.7	Age	0.0120	0.0010	11.692	<0.001
$AICc_0$ = 2662.1					
Random effect SD:					
Year = 0.0002					
Forest District = 1.7468					
***F. sylvatica* (P)**	(Intercept)	1.4128	0.6921	2.041	0.041
obs. = 48	log1p(Biomass)	-0.4167	0.1345	-3.098	0.002
AICc = 156.2	Age	-0.0150	0.0055	-2.728	0.006
$AICc_0$ = 179.8					
Random effect SD:					
Year = 7.635e-05					
Forest District = 1.086e+00					
***C. avium* (P)**	(Intercept)	0.2344	1.1882	0.197	0.844
obs. = 46	log1p(Biomass)	-0.6831	0.2230	-3.063	0.002
AICc = 102.9	Age	-0.0098	0.0051	-1.924	0.054
$AICc_0$ = 119.0					
Random effect SD:					
Year = 0.0002					
Forest District = 2.1623					
***P. cerasifera* (P)**	(Intercept)	1.9803	2.6217	0.755	0.450
obs. = 48	log1p(Biomass)	-0.3611	0.0828	-4.360	<0.001
AICc = 201.5	Age	-0.0306	0.0063	-4.839	<0.001
$AICc_0$ = 239.6					
Random effect SD:					
Year = 3.0500					
Forest District = 3.9320					
***R. pseudoacacia* (P)**	(Intercept)	0.1305	0.7273	0.179	0.858
obs. = 48	log1p(Biomass)	0.2382	0.0436	5.468	<0.001
AICc = 349.2					

$AICc_0$ = 378.2					
Random effect SD:					
Year = 1.1621					
Forest District = 0.4018					
***P. serotina* (P)**	(Intercept)	-0.5502	0.5923	-0.929	0.353
obs. = 48	log1p(Biomass)	0.4406	0.0441	9.984	<0.001
AICc = 375.9					
$AICc_0$ = 482.9					
Random effect SD:					
Year = 0.4259					
Forest District = 1.1021					
***Q. robur* (P)**	(Intercept)	-3.3147	1.5137	-2.190	0.029
obs. = 48	log1p(Biomass)	0.3910	0.1366	2.862	0.004
AICc = 84.3					
$AICc_0$ = 92.0					
Random effect SD:					
Year = 1.9762					
Forest District = 0.3335					
***A. pseudoplatanus* (ZI-P)**	(Intercept)	3.5762	0.6485	5.515	<0.001
obs. = 48	log1p(Biomass)	0.2542	0.0239	10.649	<0.001
AICc = 1091.4	Age	-0.0144	0.0020	-7.091	<0.001
$AICc_0$ = 1230.1	Zero inflation:(Intercept)	-0.2163	0.4115	-0.526	0.599
Random effect SD:					
Year = 0.4081					
Forest District = 1.2898					
Zero inflation: Year = 0.2957					
Zero inflation: F. Dist. = 0.3696					
***A. platanoides* (P)**	(Intercept)	1.6782	0.9369	1.791	0.073
obs. = 48	log1p(Biomass)	0.8234	0.0533	15.437	<0.001
AICc = 390.8	Age	-0.0424	0.0040	-10.465	<0.001
$AICc_0$ = 860.0					
Random effect SD:					
Year = 1.1860					
Forest District = 1.1650					

***A. campestre* (P)**	(Intercept)	-4.7614	2.3647	-2.014	0.044
obs. = 48	log1p(Biomass)	0.5304	0.0316	16.801	<0.001
AICc = 534.8	Age	0.0201	0.0014	14.010	<0.001
$AICc_0$ = 1032.8					
Random effect SD:					
Year = 0.0009					
Forest District = 4.3038					
***F. excelsior* (ZI-P)**	(Intercept)	1.7946	0.7872	2.280	0.023
obs. = 48	log1p(Biomass)	0.1686	0.0270	6.244	<0.001
AICc = 376	Age	0.0099	0.0025	4.035	<0.001
$AICc_0$ = 462.6	Zero inflation:(Intercept)	0.0570	0.5797	0.098	0.922
Random effect SD:					
Year = 1.1860					
Forest District = 1.1650					
Zero inflation: Year = 0.0001					
Zero inflation: F. Dist. = 1.0462					
***U. minor* (P)**	(Intercept)	0.4790	1.0116	0.474	0.636
obs. = 48	log1p(Biomass)	0.3392	0.0547	6.207	<0.001
AICc = 270.4	Age	-0.0151	0.0035	-4.281	<0.001
$AICc_0$ = 312.7					
Random effect SD:					
Year = 1.5468					
Forest District = 0.6283					
***S. nigra* (ZI-P)**	(Intercept)	1.5511	0.6754	2.297	0.022
obs. = 48	log1p(Biomass)	0.3354	0.0598	5.611	<0.001
AICc = 409.7	Age	-0.0104	0.0030	-3.406	0.001
$AICc_0$ = 448.3	Zero inflation:(Intercept)	-0.5272	0.3868	-1.363	0.173
Random effect SD:					
Year = 3.735e-05					
Forest District = 1.311e+00					
Zero inflation: Year = 3.488e-06					
Zero inflation: F. Dist. = 1.089e-04					
***C. avellana* (P)**	(Intercept)	-2.6338	0.8984	-2.932	0.003
obs. = 48	log1p(Biomass)	0.4225	0.1004	4.207	<0.001

AICc = 114.1	Age	0.0109	0.0077	1.429	0.153
$AICc_0$ = 136.2					
Random effect SD:					
Year = 0.1879					
Forest District = 0.5619					
***E. europaeus* (P)**	(Intercept)	-5.4839	1.2062	-4.546	<0.001
obs. = 48	log1p(Biomass)	0.6123	0.1019	6.009	<0.001
AICc = 138.7	Age	0.0246	0.0046	5.402	<0.001
$AICc_0$ = 225.9					
Random effect SD:					
Year = 0.8794					
Forest District = 1.4601					
***C. rhipidophylla* (P)**	(Intercept)	-6.1803	1.3428	-4.603	<0.001
obs. = 48	log1p(Biomass)	0.4463	0.0785	5.686	<0.001
AICc = 215.2	Age	0.0374	0.0065	5.775	<0.001
$AICc_0$ = 305.0					
Random effect SD:					
Year = 0.0001					
Forest District = 2.0804					
***F. alnus* (P)**	(Intercept)	-0.3771	1.5743	-0.240	0.811
obs. = 48	log1p(Biomass)	0.2519	0.1215	2.073	0.038
AICc = 126.2	Age	-0.0191	0.0070	-2.723	0.006
$AICc_0$ = 134.7					
Random effect SD:					
Year = 2.1091					
Forest District = 0.8901					

Abbreviations: **SE** – standard error; **z** – z-test statistic; **Pr(>|z|)** – p-value; **AICc** – Akaike's Information Criterion; **$AICc_0$** – AICc of null model; **SD** – standard deviation; **P** – Poisson distribution; **ZI-P ─** zero-inflation Poisson distribution; **NB ─** negative binomial distribution

Table S13. List of seedling species observed with their frequency [%]. Values above 10% were bolded (species assessed in the study).

Species	***P. serotina* poor**	***P. serotina* rich**	***R. pseudoacacia* poor**	***R. pseudoacacia* rich**

Acer campestre L.	0.0	2.1	0	6.3
Acer platanoides L.	0.0	0.0	0.0	4.2
Acer pseudoplatanus L.	4.3	**18.3**	2.1	**12.5**
Betula pendula Roth	6.4	0.0	2.1	0
Carpinus betulus L.	0.0	4.2	0.0	4.2
Crataegus monogyna Jacq.	0.0	2.1	0.0	2.1
Fagus sylvatica L.	0.0	2.1	0.0	4.2
Frangula alnus Mill.	8.5	0.0	2.1	0.0
Fraxinus excelsior L.	0.0	4.2	0.0	8.3
Pinus sylvestris L.	**27.7**	4.2	**16.7**	2.1
Prunus cerasifera Ehrh.*	2.1	0.0	0.0	0.0
Prunus domestica L.	0.0	0.0	0.0	2.1
Prunus serotina Ehrh.*	**59.6**	**29.2**	**14.6**	4.2
Quercus petraea (Matt.) Liebl.	**21.3**	**22.9**	**14.6**	**20.8**
Quercus robur L.	2.1	0.0	0.0	2.1
Quercus rubra L.*	2.1	0.0	4.2	6.3
Robinia pseudoacacia L.*	2.1	2.1	**18.8**	**10.4**
Sambucus nigra L.	0.0	4.2	0.0	2.1
Sorbus aucuparia L.	6.4	0.0	0.0	0.0
Tilia cordata Mill.	0.0	2.1	0.0	2.1
Ulmus minor Mill.	0.0	2.1	0.0	2.1

*Non-native species

Table S14. The parameters of Generalized Linear Mixed-Effect Models for the impact of *P. serotina* aboveground biomass (AB) on seedlings density on nutrient-poor sites. Abbreviation in parentheses for each species indicates the distribution of dependent variable.

Response	Variable	Estimate	SE	z	Pr(<|z|)

***P. serotina* (P)**	(Intercept)	1.0930	1.0872	1.005	0.315
obs. = 47	log1p(Biomass)	0.9838	0.0473	20.805	<0.001
AICc = 678.4	Age	-0.0150	0.0015	-10.145	<0.001
$AICc_0$ = 1327.3					
Random effect SD:					
Year = 0.001619					
Forest District = 2.134065					
***P. sylvestris* (P)**	(Intercept)	1.7466	0.9253	1.888	0.059
obs. = 47	log1p(Biomass)	-0.3907	0.1886	-2.072	0.038
AICc = 133.1	Age	-0.0288	0.0108	-2.664	0.008
$AICc_0$ = 141.1					
Random effect SD:					
Year = 7.556e-05					
Forest District = 1.027e+00					
***Q. petraea* (P)**	(Intercept)	-2.6130	1.0098	-2.588	0.001
obs. = 47	log1p(Biomass)	0.9318	0.2116	4.404	<0.001
AICc = 159.9					
$AICc_0$ = 181.7					
Random effect SD:					
Year = 0.0001796					
Forest District = 1.4877061					

Abbreviations: **SE** – standard error; **z** – z-test statistic; **Pr(>|z|)** – p-value; **AICc** – Akaike's Information Criterion; **$AICc_0$** – AICc of null model; **SD** – standard deviation; **P** – Poisson distribution

Table S15. The parameters of Generalized Linear Mixed-Effect Models for the impact of *P. serotina* aboveground biomass (AB) on seedlings density on nutrient-rich sites. Abbreviation in parentheses for each species indicates the distribution of dependent variable.

Response	Variable	Estimate	SE	z	Pr(<|z|)
***P. serotina* (P)**	(Intercept)	-6.7327	2.7253	-2.470	0.010

obs. = 48	log1p(Biomass)	1.3818	0.1334	10.360	<0.001
AICc = 219.9	Age	0.0301	0.0024	12.650	<0.001
$AICc_0$ = 450.9					
Random effect SD:					
Year = 4.168e+00					
Forest District = 3.036e-05					
***A. pseudoplatanus* (P)**	(Intercept)	3.8849	0.8947	4.342	<0.001
obs. = 48	log1p(Biomass)	-0.5484	0.1138	-4.819	<0.001
AICc = 590.1	Age	-0.0411	0.0059	-7.012	<0.001
$AICc_0$ = 690.2					
Random effect SD:					
Year = 0.8096					
Forest District = 0.8535					

Abbreviations: **SE** – standard error; **z** – z-test statistic; **Pr(>|z|)** – p-value; **AICc** – Akaike's Information Criterion; **$AICc_0$** – AICc of null model; **SD** – standard deviation; **P** – Poisson distribution

Table S16. The parameters of Generalized Linear Mixed-Effect Models for the impact of *R. pseudoacacia* aboveground biomass (AB) on seedlings density on nutrient-poor sites. Abbreviation in parentheses for each species indicates the distribution of dependent variable.

Response	Variable	Estimate	SE	z	Pr(<|z|)
***R. pseudoacacia* (P)**	(Intercept)	-0.5832	2.0412	-0.286	0.775
obs. = 48	log1p(Biomass)	0.8404	0.1298	6.477	<0.001
AICc = 130.5	Age	-0.0532	0.0076	-6.980	<0.001
$AICc_0$ = 201.4					
Random effect SD:					
Year = 2.271					
Forest District = 2.042					
***P. sylvestris* (P)**	(Intercept)	2.8190	1.2623	2.233	0.030
obs. = 48	log1p(Biomass)	-0.2992	0.1314	-2.278	0.020

AICc = 212.8	Age	-0.0564	0.0123	-4.602	<0.001
$AICc_0$ = 256.8					
Random effect SD:					
Year = 1.3757					
Forest District = 0.3654					

Abbreviations: **SE** – standard error; **z** – z-test statistic; **Pr(>|z|)** – p-value; **AICc** – Akaike's Information Criterion; **$AICc_0$** – AICc of null model; **SD** – standard deviation; **P** – Poisson distribution

Table S17. The parameters of Generalized Linear Mixed-Effect Models for the impact of *R. pseudoacacia* aboveground biomass (AB) on seedlings density on nutrient-rich sites. Abbreviation in parentheses for each species indicates the distribution of dependent variable.

Response	Variable	Estimate	SE	z	Pr(<|z|)
***Q. petraea* (P)**	(Intercept)	-9.0765	2.2890	-3.965	<0.001
obs. = 48	log1p(Biomass)	-0.1987	0.0753	-2.641	0.010
AICc = 154.6	Age	0.0698	0.0111	6.287	<0.001
$AICc_0$ = 288.7					
Random effect SD:					
Year = 2.481					
Forest District = 1.320					
***A. pseudoplatanus* (P)**	(Intercept)	2.5764	1.5006	1.717	0.090
obs. = 48	log1p(Biomass)	-0.6233	0.1498	-4.162	<0.001
AICc = 477.8	Age	-0.0329	0.0048	-6.817	<0.001
$AICc_0$ = 604.9					
Random effect SD:					
Year = 2.197e+00					
Forest District = 9.566e-05					

Abbreviations: **SE** – standard error; **z** – z-test statistic; **Pr(>|z|)** – p-value; **AICc** – Akaike's Information Criterion; **$AICc_0$** – AICc of null model; **SD** – standard deviation; **P** – Poisson distribution

References

Alberti G, Candido P, Peressotti A, Turco S, Piussi P, Zerbi G (2005) Aboveground biomass relationships for mixed ash (*Fraxinus excelsior* L. and *Ulmus glabra* Hudson) stands in Eastern Prealps of Friuli Venezia Giulia (Italy). Annals of Forest Science 62: 831–836. https://doi.org/10.1051/forest:2005089

Baker M, King R, Kahle D (2020) An Introduction to TITAN2. Version 2.4.3. https://CRAN.R-project.org/package=TITAN2

Brown JK (1976) Estimating shrub biomass from basal stem diameters. Canadian Journal of Forest Research: 153–158. https://doi.org/10.1139/x76-019

Forrester DI, Tachauer IHH, Annighoefer P, Barbeito I, Pretzsch H, Ruiz-Peinado R, Stark H, Vacchiano G, Zlatanov T, Chakraborty T, Saha S, Sileshi GW (2017) Generalized biomass and leaf area allometric equations for European tree species incorporating stand structure, tree age and climate. Forest Ecology and Management 396: 160–175. https://doi.org/10.1016/j.foreco.2017.04.011

Jagodziński A, Dyderski M, Gęsikiewicz K, Horodecki P (2018) Tree- and Stand-Level Biomass Estimation in a *Larix decidua* Mill. Chronosequence. Forests 9: 587. https://doi.org/10.3390/f9100587

Jagodziński AM, Dyderski MK, Gęsikiewicz K, Horodecki P (2019) Effects of stand features on aboveground biomass and biomass conversion and expansion factors based on a *Pinus sylvestris* L. chronosequence in Western Poland. European Journal of Forest Research 138: 673–683. https://doi.org/10.1007/s10342-019-01197-z

Zasada M (2017) Raport końcowy z tematu badawczego "Ekologiczne, gospodarcze i urządzeniowe konsekwencje występowania wybranych gatunków drzew obcych w Polsce" realizowanego w latach 2013-2017 przez Samodzielną Pracownię Dendrometrii i Nauki o Produkcyjności Lasu na zlecenie Dyrekcji Generalnej Lasów Państwowych w Warszawie. SGGW, Warszawa

Publikacja 3.

Sebastian Bury, Marcin K. Dyderski

Invasive *Prunus serotina* and *Robinia pseudoacacia* impact on understory vegetation is species-, habitat-, and season-specific

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Research Article

Invasive *Prunus serotina* and *Robinia pseudoacacia* impact on understory vegetation is species-, habitat-, and season-specific

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Abstract

Although the impact of invasive species on understory diversity has been extensively studied, most authors have compared invaded and non-invaded stands. Various authors have demonstrated different negative, positive, or no impacts of invasive trees on understory vegetation biodiversity. In our study, we aimed to assess the relationship between alpha diversity and species composition of the understory and the increasing aboveground biomass of two invasive trees, *Prunus serotina* and *Robinia pseudoacacia*. We assessed this relationship for two seasons (spring and summer) and two habitats (nutrient-rich habitats with oaks *Quercus petraea* and *Q. robur* and nutrient-poor habitats with Scots pine *Pinus sylvestris*) separately. We demonstrated a statistically significant relationship between understory species composition and increasing biomass of both invaders in both habitats in both seasons, except in nutrient-rich sites with *R. pseudoacacia*. In summer, we found indicator species for both invasive species in both habitats, while in spring, only for the nutrient-rich habitat with *P. serotina*. In nutrient-rich habitats, we did not find any significant effect of increasing *P. serotina* biomass on alpha diversity indices. In nutrient-poor habitats, *P. serotina* biomass was positively correlated with taxonomic and functional diversity but not significantly related to phylogenetic diversity. In summer, *R. pseudoacacia* biomass was positively correlated with taxonomic diversity in poor habitats and with functional dispersion but negatively correlated with mean pairwise phylogenetic distance. In nutrient-rich habitats, we observed a positive relationship between *R. pseudoacacia* biomass and phylogenetic diversity and a negative relationship with functional dispersion. Therefore, our results indicated high variability and context-dependence of invader impacts, related to invader species, understory species, habitat, and season. We confirmed that the relationship between invader biomass and nitrophilous, ruderal species is positive, while it is negative with forest specialists, especially on nutrient-poor sites.

Key words: Black cherry, black locust, functional diversity, indicator taxa, invasion ecology, phylogenetic diversity, seasonality, taxonomic diversity

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Introduction

Invasive species are one of the greatest threats to biodiversity (Richardson et al. 2000; Brondízio et al. 2019; Roy et al. 2024). Invasive trees as 'transformers' (*sensu* Richardson et al. 2000) can significantly change native ecosystems (Crooks 2002; Corenblit et al. 2014; Jagodziński et al. 2024). The changes in, e.g., nutrient cycling (Rice et al. 2004; Aerts et al. 2017) or light availability (Starfinger et al. 2003; Dyderski and Jagodziński 2019; García et al. 2023) can positively impact some

understory plant species, but some of them can retreat from transformed, invaded habitats (Chabrerie et al. 2008; Langmaier and Lapin 2020; Woziwoda et al. 2021; Bury and Dyderski 2025a, b).

In European forests, *Prunus serotina* Ehrh. (black cherry) and *R. pseudoacacia* L. (black locust) are among the most widespread non-native tree species (Wagner et al. 2017; Brus et al. 2019). *Prunus serotina* in Central European conditions is mostly a shrub or low tree (Starfinger et al. 2003; Bury and Dyderski 2024b, 2025a; Engel et al. 2024; Nyssen et al. 2024) and is mostly dispersed via zoochory and barochory (Starfinger et al. 2003; Deckers et al. 2008). This species does not have nitrogen-fixing abilities and is an early/mid-successional species mostly occurring in stand gaps (Godefroid et al. 2005; Closset-Kopp et al. 2007). *Robinia pseudoacacia* has different growing forms. It can be a shrub or a low or high tree (Bury and Dyderski 2025a). This pioneer species (Cierjacks et al. 2013; Vítková et al. 2017; Martin 2019) has nitrogen-fixing abilities (Rice et al. 2004; Vítková et al. 2017) and is mainly dispersed via barochory and anemochory (Vítková et al. 2017). Additionally, next to sexual, also vegetative reproduction by root suckers is an important way to settle in a new place (Cierjacks et al. 2013; Bouteiller et al. 2023) (Fig. 1a).

Vascular plants are the most studied taxonomic group in the case of the invasive trees effect on biodiversity (Vilà et al. 2024). Up to 2022, Wohlgemuth et al. (2022) identified 720 cases of different non-native trees effects on different vascular plant diversity attributes. Among them, 191 cases show non-significant relationships, 14 negative, and 21 positive effects of *P. serotina* on vascular plant diversity attributes. For *R. pseudoacacia*, 144 studies show non-significant relationships, 19 decreasing, and 31 increasing effects (Wohlgemuth et al. 2022). However, there is a noticeable difference in the study of the impact of both *P. serotina* and *R. pseudoacacia* at the species and community levels. According to the recent review by Vilà et al. (2024), there are only a few studies that focus on examining the impact of the abovementioned invasive tree species at the species level (Halarewicz and Pruchniewicz 2015). On the community level for *P. serotina*, among 90 studies about the impact on plants, 70 are about plant diversity; for *R. pseudoacacia*, among 46 studies, 32 are about plant diversity (Vilà et al. 2024). However, some previous studies revealed both negative and positive effects of studied invasive trees on individual species (e.g., Chabrerie et al. 2008; Halarewicz and Pruchniewicz 2015). There are important studies focused on *P. serotina* and *R. pseudoacacia* cover as quantitative indicators. Most of the studies about the impact of both *R. pseudoacacia* (Rahmonov 2009; Qiu et al. 2010; Benesperi et al. 2012; Trentanovi et al. 2013; Lazzaro et al. 2018; Sitzia et al. 2018; Gentili et al. 2019; Slabejová et al. 2019, 2023; Dyderski and Jagodziński 2021) and *P. serotina* (Verheyen et al. 2007; Halarewicz and Żołnierz 2014; Gentili et al. 2019; Dyderski and Jagodziński 2021) on understory plant diversity focused on comparing invaded and non-invaded stands. In contrast, only a few studies assessed the effects of invasive trees along their abundance gradient. Abundance gradient is important, as it not only reveals the thresholds of impact (Dickie et al. 2011) but also can be used as a space-for-time substitution in predicting the effects of invasive species spread (López-Núñez et al. 2017). There are only a few studies on *P. serotina* (Chabrerie et al. 2008, 2010; Bury and Dyderski 2024a) and *R. pseudoacacia* (Montecchiari et al. 2020) per capita effect on understory plants. For *P. serotina*, we showed a small positive relationship between the proportion of its biomass and species and functional richness. However, the study concerned a single forest complex, which is the Wielkopolska National Park, under

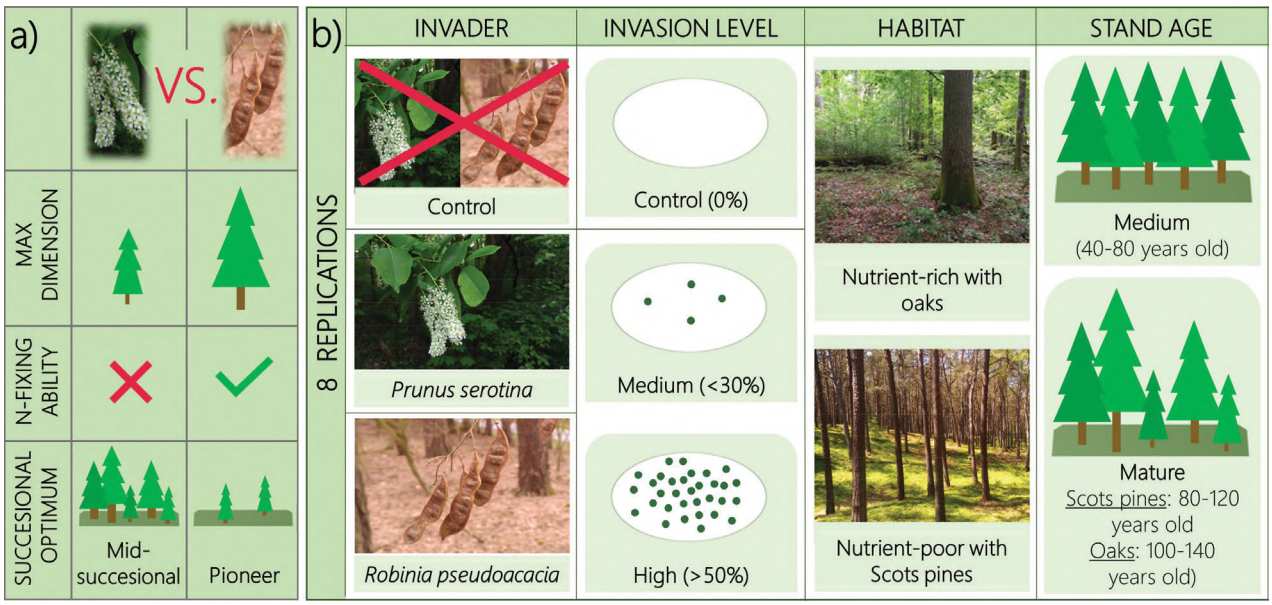

Figure 1. Comparison of studied invasive tree species (**a**) and study design (**b**).

a nature conservation regime. It is more difficult to apply the conclusions drawn from the cited work on a larger spatial scale, even within the same region. Previous studies revealed that abundance moderates the effects of *P. serotina* and *R. pseudoacacia* on natural regeneration (Bury and Dyderski 2025a) and bryophytes (Bury and Dyderski 2025b). Studies on other invasive trees revealed negative (García et al. 2023) or non-linear (initial increase and subsequent decline in species richness) (Dickie et al. 2011) impact of invader biomass on understory diversity.

The vegetation of the understory is not the same throughout the entire growing season (Rautiainen et al. 2011). These differences are determined by phenology (Miller et al. 1997; Kudo et al. 2008), as many species have their peak flowering in spring, when the trees have not yet developed leaves (Heinrich 1976; Kudo et al. 2008; Heberling et al. 2019; Rawlik et al. 2023). A lot of light reaches during this time, which is necessary for the development of flowers and fruits (Stephenson 1981). The existence of many plant species, their biology, and their ecology depend on other organisms, e.g., pollinating insects (Kudo et al. 2008), which also have different activities depending on the seasons (Li et al. 2025). Seasonal changes in the species composition and biomass can vary strongly in individual habitats. The peak occurrence of geophytes occurs in spring, and summer is the period of dominance of species that tolerate shading better (Rawlik et al. 2023). However, little is known about how invasive trees, through the environmental changes they cause, can have a different impact on the biodiversity of the understory plants growing in temperate forests in spring and summer. Most previous studies focused mainly on summer vegetation, neglecting the spring aspect, abundant in forest specialists (Hermy et al. 1999).

Numerous previous studies proved that high biological diversity has a positive impact on the stability and durability of forest ecosystems (Hisano et al. 2018; Conradi et al. 2020). However, many works only discuss the issue of species richness. In addition to taxonomic diversity, which describes the number and abundance of species, it is worth delving deeper into the role of these species in ecosystems, related to their unique functional traits (functional diversity) (Violle et al. 2007), and the diversity of their evolutionary origins (phylogenetic diversity) (Tucker et

al. 2017). Functional and phylogenetic (Swenson and Enquist 2009) diversities (Violle et al. 2007; Laliberté and Legendre 2010; Hao et al. 2018) also indicate the resilience of the different components of ecosystems (Buckley et al. 2023).

Due to the large differences between nutrient-poor and nutrient-rich habitats in Central Europe, it is worth examining these habitats separately (Bury and Dyderski 2024b, 2025a). This will allow for better adaptation of protective treatments to the needs of specific plant communities (Nyssen and Vanhellemont 2016; Sádlo et al. 2017; Engel et al. 2024; Nyssen et al. 2024). Both of these habitats are characterized by a specific species composition. Plants adapted to the soil fertility grow there. Nutrient-poor stands are mostly dominated by coniferous trees, e.g., *P. sylvestris*, while nutrient-rich stands are dominated by deciduous trees, e.g., *Quercus* spp. However, these differences concern not only the tree stand level but also the understory vegetation (Ellenberg and Leuschner 2010; Mucina et al. 2016). In the context of invasion ecology, previous studies proved that changes caused by invasive woody species may be more negative in poor habitats (Chmura 2004; Halarewicz 2011), indicating context dependence (Novoa et al. 2020; Sapsford et al. 2020).

In this paper, we aimed to assess the impact of two invasive tree species, *P. serotina* and *R. pseudoacacia*, on understory vascular plant biodiversity at three levels: taxonomic, functional, and phylogenetic, as well as species composition. Furthermore, we assessed whether there are indicator species for increasing invader aboveground biomass. We hypothesized that (H1) we will find changes in vascular plant alpha diversity and species composition along invader aboveground biomass (Dickie et al. 2011; García et al. 2023; Bury and Dyderski 2024a). (H2) We hypothesized that the relationships between vascular plant diversity and invader biomass will be different between *P. serotina* and *R. pseudoacacia*, and additionally, we will find different taxa indicating invader aboveground biomass increase (Bury and Dyderski 2025a). (H3) Furthermore, we supposed that there will be differences in diversity-invader biomass relationships between nutrient-poor and nutrient-rich sites (Chmura 2004; Halarewicz 2011; Bury and Dyderski 2025a). (H4) Finally, we expected differences in patterns between spring and summer surveys. Checking the differences between spring, a season when many geophytes reach optimal growth, and summer–a season when different taxa (mostly hemicryptophytes) emerge (Rawlik et al. 2023)–should answer the question: which seasonal aspect of vegetation is more threatened by an increase in invasive tree biomass? We expect that in the spring, when canopy foliage has not yet emerged, the impact of the studied invasive trees will be lower (Heinrich 1976; Kudo et al. 2008; Czapiewska et al. 2019). Our work addresses an important and still poorly understood phenomenon called the per capita effect, or the scaled effect of invasion (Parker et al. 1999; Schooler et al. 2006; Bury and Dyderski 2024a). More specifically, in our research, we focus on aboveground biomass of invasive trees and how it affects the relationship between invasive trees and understory (Dickie et al. 2011; García et al. 2023; Bury and Dyderski 2024a). Additionally, we have placed our research in two contexts: habitat, which answers the question of where invasive species have a more or less significant impact, and seasonal, which answers the question of when the studied invasive species have a more or less significant impact on understory vegetation. The habitat context (Chmura 2004; Halarewicz 2011; Bury and Dyderski 2024a) is better known than the seasonal one. The seasonality we studied adds a novel perspective on the relationship between invasive trees and the understory vegetation.

Methods

Study design and study area

We conducted our study in the managed forests in Western Poland (Czerniejewo, Łopuchówko, Babki, Konstantynowo, and Jarocin Forest Districts (i.e., spatial administration units)). The climatic conditions are typical for a warm-summer humid continental climate with an annual temperature of 8.5 °C and mean annual precipitation of 500–550 mm (BDL 2024) (Suppl. material 1: fig. S1).

In the field, we searched for plots non-invaded (control) and invaded by *P. serotina* or *R. pseudoacacia*. Initially, we used canopy cover as an abundance indicator because it was easier to assess in the field and did not require time-consuming measurements necessary to estimate biomass. We used two classes of cover to distinguish plots with medium cover (< 30%) and high cover (> 50%), which formed the invasion gradient, based on species biomass. Additionally, we accounted for two different habitat and stand maturity contexts. We established our plots in nutrient-poor and nutrient-rich habitats. Nutrient-poor sites included plant communities dominated by *P. sylvestris*, i.e., *Leucobryo-Pinetum* W. Mat. (1962) 1973 communities or secondary *P. sylvestris* forests. Nutrient-rich sites included communities dominated by *Q. petraea* and *Q. robur*, i.e., different subtypes of *Galio sylvatici-Carpinetum betuli* Oberd. 1957 communities or secondary *Quercus* spp. forests (Bury and Dyderski 2025a). Some of our plots had characteristics of slightly poorer communities or slightly more fertile ones, e.g., *Potentillo albae-Quercetum* Libb. 1933 and *Querco-roboris Pinetum* Mat. et Polak. 1955 s.l. We also selected plots in two stand age classes. We distinguished medium-aged stands (stands in the middle of rotation age, 40–80 years old) and mature stands (close to rotation age; for Scots pines, 80–120 years old; for oaks, 100–140 years old). Medium-aged stands have simpler structures–trees have a similar diameter at breast height (DBH) and height–compared to more structurally diverse, mature stands. Mature stands grow more slowly than middle-aged stands because they have already reached the peak of growth (Jiang et al. 2017; Li et al. 2024). The older the tree stands, the greater the biodiversity, which is related to the greater availability of light correlated with the smaller stem density (Jagodziński and Oleksyn 2009; Felton et al. 2010; Conradi et al. 2020). In total, we established 160 plots (32 control plots, 64 plots with *R. pseudoacacia*, and 64 plots with *P. serotina*). To avoid the spatial autocorrelation, plots of individual variants were at least 5 km apart (plot variant = invader × invasion level × habitat × stand age) (Bury and Dyderski 2025a) (Fig. 1b).

Assessment of invader aboveground biomass

We assessed invader aboveground biomass using the same methodology as Bury and Dyderski (2025a, b). After an initial survey based on the cover of studied invasive species (subsection 2.1), we measured tree stand structures. We measured the DBH of all trees ≥ 1.3 m height on 102 plots in 2021 and 2022 (García et al. 2023; Bury and Dyderski 2025a). On the other 58 plots in 2022 and 2023, we measured the DBH of trees > 5 cm DBH, and we counted trees thinner than 5 cm. Then, we used the dataset for 102 plots, and for all tree species, we estimated the mean DBH for trees thinner than 5 cm (Bury and Dyderski 2025a) (Suppl. material 1: table S1). We decided to use this method to reduce time-consuming measurements of numerous thin individuals with low variability of DBH and not to assume a midpoint of DBH range from 0 to 5 cm (2.5 cm) for biomass calculation as in previous studies

(Dyderski and Jagodziński 2019). We used published allometric models (Suppl. material 1: table S2) to calculate invader aboveground biomass (Brown 1976; Alberti et al. 2005; Forrester et al. 2017; Zasada 2017; Jagodziński et al. 2018, 2019) (Fig. 2). *Prunus serotina* aboveground biomass on nutrient-poor sites ranged from 0.18 to 47.11 Mg ha^{-1} (mean: 7.34 ± 8.75 Mg ha^{-1}) and on nutrient-poor sites from 0.19 to 27.39 Mg ha^{-1} (mean: 6.68 ± 7.24 Mg ha^{-1}). *Robinia pseudoacacia* aboveground biomass on nutrient-poor sites ranged from 0.22 to 153 Mg ha^{-1} (mean: 20.91 ± 31.69 Mg ha^{-1}) and on nutrient-rich sites from 0.82 to 278.24 Mg ha^{-1} (mean: 50.77 ± 70.37 Mg ha^{-1}) (Suppl. material 1: table S4) (Bury and Dyderski 2025a).

Understory vegetation assessments

We used the modified nine-scaled Braun-Blanquet method (**r** – 1–2 ind.; **+** – <1%; **1** – 1–3%; **2m** – 3–10%; **2a** – 10–18%; **2b** – 18–25%; **3** – 25–50%; **4** – 50–75%; **5** – > 75%) to assess the cover of particular understory species of vascular plants. We assessed both herbaceous and woody plants (up to 0.5 m height) on four randomly distributed squared 25 m^2 subplots. We conducted an understory survey in the spring (May) and summer (July) of 2021, 2022, and 2023. We aggregated the results at the plot level by averaging species cover from four subplots (Fig. 2).

Alpha diversity indices calculation

In spring, we found 183 vascular plant species, while in summer, we found 167 (in total, 205 species). We calculated taxonomic alpha diversity using two indices: Shannon's diversity index, calculated by the diversity() function, and species richness, calculated by the specnumber() function, both from the vegan package (Oksanen et al. 2018). For phylogenetic alpha diversity, we calculated Faith's phylogenetic diversity (PD) and mean pairwise distance (MPD), using the ses.pd() and ses.mpd() functions from the picante package (Kambel et al. 2010). We acquired a phylogenetic tree by using the phylo.maker() function in the V.Phylomaker2 package (Jin and Qian 2022). Both PD and MPD were standardized to exclude

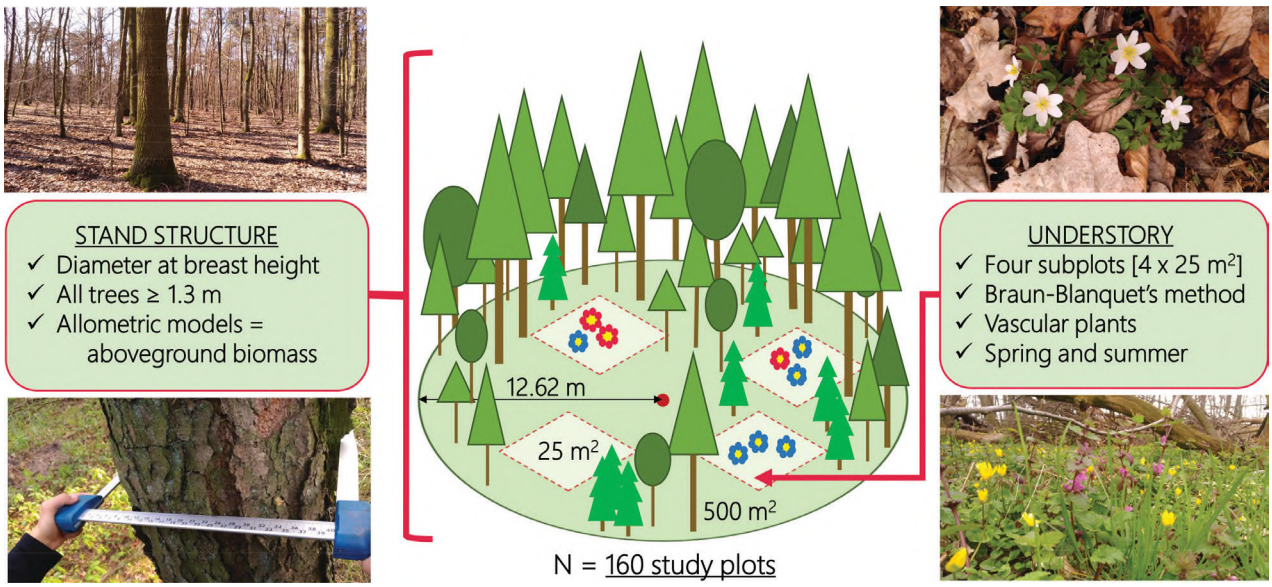

Figure 2. Graphical presentations of field surveys, including both stand structure measurements and understory vegetation surveys.

the effect of species richness on estimating phylogenetic diversity. For functional alpha diversity, we acquired functional traits for species present in our study plots from several databases, i.e., LEDA (Kleyer et al. 2008), BIEN (Maitner et al. 2018), BioFlor (Klotz et al. 2002), and Pladias (Wild et al. 2019). Additionally, we acquired ecological indicator values (EIVs) from Ellenberg and Leuschner (2010). Due to the low incompleteness of trait data (Suppl. material 1: table S5), we decided to impute missing values with the missForest package (Stekhoven and Buhlmann 2012), supported by phylogenetic eigenvectors (Diniz-Filho et al. 1998), calculated using the acquired phylogenetic tree. As functional diversity is species richness-dependent, we assessed the standardized (Czortek et al. 2021) functional richness (FRic) and functional dispersion (FDis), using the dbFD() function from the FD package (Laliberté and Legendre 2010). We followed the standardization algorithm provided by Czortek et al. (2021), where we calculated the null model based on species composition randomized using the randomizeMatrix() function from the picante package (Kambel et al. 2010) in 10000 iterations. The standardized indicator sesFRic was calculated using the formula: $sesFRic = FRic_R - FRic_{null} / SD(FRic_{null})$, where: $FRic_R$ is the observed *FRic* value, $FRic_{null}$ is the mean *FRic* value of the null model, and $SD(FRic_{null})$ is the standard deviation of the *FRic* null model. The standardized indicator *sesFDis* was calculated using the formula: $sesFDis = FDis_R - FDis_{null} / (FDis_{null})$, where: $FDis_R$ is the observed *FDis* value, $FDis_{null}$ is the mean *FDis* value of the null model, and $SD(FDis_{null})$ is the standard deviation of the *FDis* null model. As calculations of *FDis* and *FRic* are meaningful only for plant communities with at least three species, we excluded one plot for the spring dataset (control plot on nutrient-poor site) with only two species from analyses for these alpha diversity metrics. To characterize the functional composition of understory vegetation, we calculated community-weighted means (CWMs) of functional traits and EIVs: EIV.L – Light EIV; EIV.M – Moisture EIV; EIV.N – Soil Fertility EIV; EIV.SR – Soil Reaction EIV; SLA – Specific Leaf Area [cm^2 g^{-1}]; H – Maximum height [m]; SM – Seed mass [mg].

Statistical analyses

From all analyses, we excluded one outlying study plot (nutrient-poor habitat) with *P. serotina* aboveground biomass (47.11 Mg ha^{-1}) tree times higher than the next plot in this variant (15.43), similarly to Bury and Dyderski (2025a). In all analyses we used log1p transformation (i.e., log(x+1)) of invader aboveground biomass to include sites with zero biomass and to stabilize variance in this predictor.

We used Canonical Correspondence Analysis (CCA) from the vegan package (Oksanen et al. 2018) to study the relationship between the studied invaders aboveground biomass and the vascular plant species composition of the understory. In CCA, we used invader aboveground biomass and stand age as constraints, testing the hypotheses about their impact on species composition. To test the significance of these factors, we used permutation-based ANOVA-like tests, implemented in the anova.cca() function.

We used the Threshold Indicator Taxa Analysis to check which species change their abundance over the studied invasive species biomass. We presented only those species that revealed trends with purity and reliability > 0.95 (default settings). We presented the results using the plottaxaridges() function from the TITAN2 package (Baker et al. 2023). This function creates graphs for particular species responses

along environmental gradients. These species are divided into two groups: increasers (different shapes of red color of ridges) and decliners (different shapes of grey color or blue color of ridges). The increasers are species with cover increasing with invader biomass increasing, while decliners are species with decreasing cover with invader biomass increasing. Ridges can look different for particular species. The inflection of the ridge indicates the value of the aboveground biomass of the invader where the cover of a particular species is the highest. A narrow ridge indicates small discrepancies in the data, and a wide ridge indicates large discrepancies. Z-values (numerical values that correspond to the intensity of ridge color) inform about the taxa indicator value–darker color and higher value suggest a higher indicator value. A vertical black line indicates aboveground biomass. In the case of increasers, there is a sharp increase in understory species cover, and in the case of decliners, there is a sharp decrease in understory species cover.

Finally, we used generalized linear mixed-effect models (GLMMs) (Brooks et al. 2017) to study the relationship between different invasive tree species aboveground biomass with alpha diversity metrics and CWMs of traits (SLA, SM, and H) and EIVs. In each model we also included stand age to control this variable. For each season, invasive tree species, and habitat, we developed separate models. For H and SM CWMs, we used log10 transformations of the dependent variable due to a high variability of these traits, exceeding four orders of magnitude. For species richness, we assumed a Poisson or negative binomial distribution, ensuring a lack of problems with overdispersion, while for all other variables, we assumed a Gaussian distribution due to the close-to-normal distribution of the dependent variable. We used the survey year and forest districts as random effects. We used the glmmTMB package (Brooks et al. 2017) to develop GLMMs and the dredge() function from the MuMIn package (Bartoń et al. 2017) to choose the best-fit models, reducing them to minimize values of Akaike's Information Criterion, corrected for small sample size (AICc). For each model, we stated the AICc of the final model and $AICc_0$, i.e., the AICc of the null (intercept and random effects-only model). We presented model responses using marginal responses, i.e., mean predicted values for each level of a particular predictor, calculated using the ggeffects package (Lüdecke 2018). In the results section, we present values estimated for statistically significant relationships for two points: for zero and near the maximum value of invader biomass in each variant. We used the same biomass values as in Bury and Dyderski (2025a). All mean values are followed by ± standard error.

Results

Relationships between invasive tree biomass and understory species composition

In spring we found a statistically significant relationship between species composition and invader aboveground biomass except for *R. pseudoacacia* on nutrient-rich sites (p=0.083; Fig. 3b, Table 1). On nutrient-poor sites, *Rubus idaeus*, *R. fruticosus* agg., and *P. serotina* increased their cover with an increase in *P. serotina* biomass (Fig. 3e), while species like *Moehringia trinervia*, *Fallopia convolvulus*, *Chelidonium majus*, *Impatiens parviflora*, *Geranium robertianum*, and *R. pseudoacacia* increased their cover with an increase in *R. pseudoacacia* biomass (Fig. 3a). For control plots

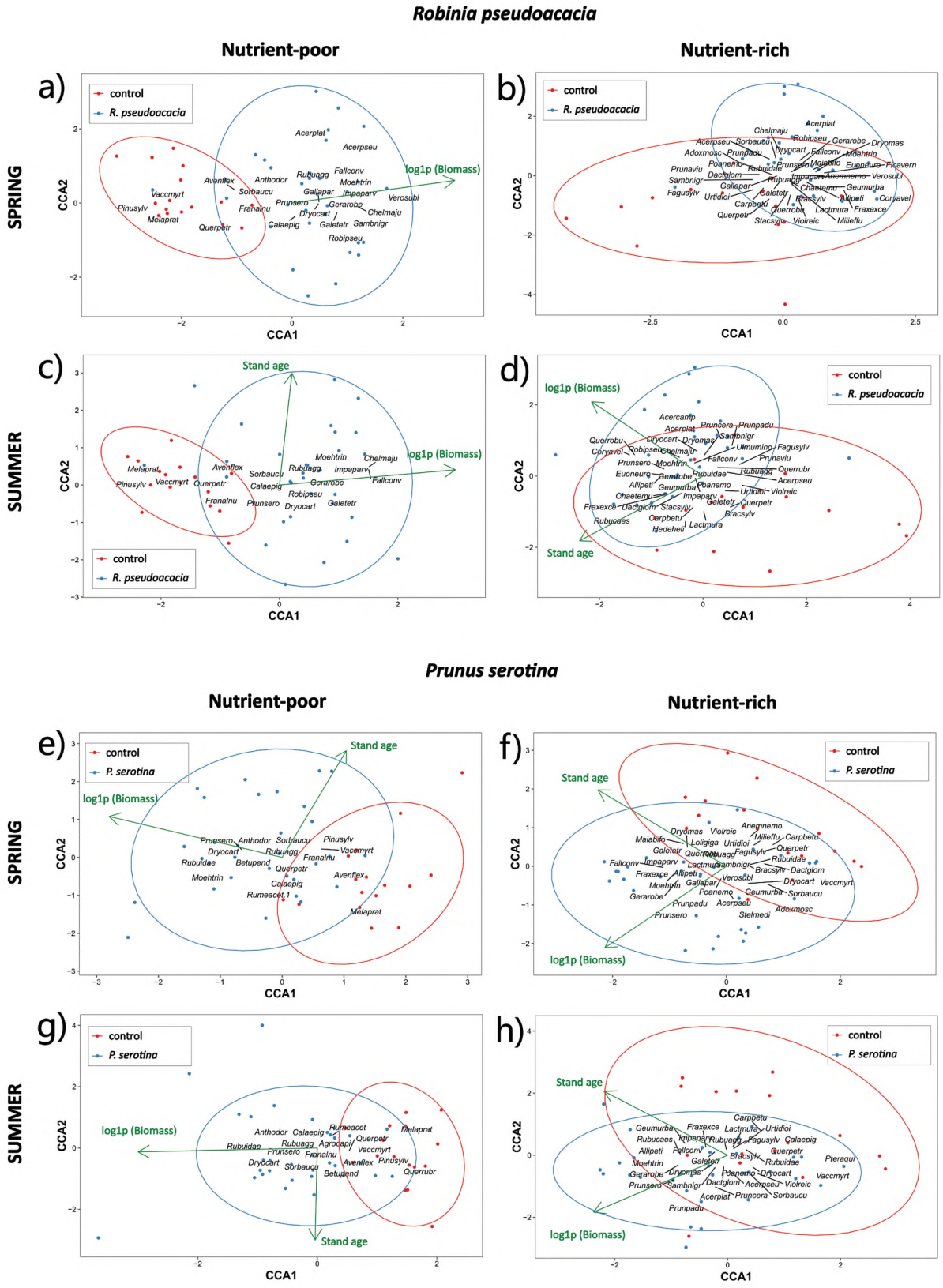

Figure 3. Canonical Correspondence Analysis (CCA) for all plot variants: *R. pseudoacacia* nutrient-poor (48 plots) and nutrient-rich sites (48 plots); *P. serotina* nutrient-rich (48 plots) and nutrient-poor sites (47 plots) for both spring and summer. For clarity, only species with a frequency > 20% were labeled. Green arrows and labels represent environmental variables (only for statistically significant results, $p < 0.05$). Red dots = control plots, blue dots = plots with *P. serotina* or *R. pseudoacacia*. Abbreviations: **log1p(Biomass)** – natural logarithm of invader aboveground biomass.

Table 1. Results of permutation-based ANOVA-like test (999 iterations) of constraint significance for CCA. Abbreviations: **log1p(Biomass)** – natural logarithm of invader aboveground biomass.

	Df	χ^2	F	Pr(>F)
SPRING				
P. serotina nutrient-poor sites (n = 47 plots)				
log1p(Biomass)	1	0.2098	2.2640	0.001
Stand age	1	0.1587	1.7132	0.012
Residual	44	4.0765		
P. serotina nutrient-rich sites (n = 48 plots)				
log1p(Biomass)	1	0.1484	1.4496	0.020
Stand age	1	0.1477	1.4421	0.017
Residual	45	4.6069		
R. pseudoacacia nutrient-poor sites (n = 48 plots)				
log1p(Biomass)	1	0.3038	2.7142	0.001
Stand age	1	0.1640	1.4656	0.122
Residual	45	5.0371		
R. pseudoacacia nutrient-rich sites (n = 48 plots)				
log1p(Biomass)	1	0.1408	1.2730	0.083
Stand age	1	1.1388	1.2545	0.105
Residual	45	4.9784		
SUMMER				
P. serotina nutrient-poor sites (n = 47 plots)				
log1p(Biomass)	1	0.1611	1.6468	0.007
Stand age	1	0.1444	1.4758	0.024
Residual	45	4.4022		
P. serotina nutrient-rich sites (n = 48 plots)				
log1p(Biomass)	1	0.2285	2.6348	0.001
Stand age	1	0.1339	1.5438	0.044
Residual	45	3.9033		
R. pseudoacacia nutrient-poor sites (n = 48 plots)				
log1p(Biomass)	1	0.3421	3.1727	0.001
Stand age	1	0.1839	1.7052	0.019
Residual	45	4.8252		
R. pseudoacacia nutrient-rich sites (n = 48 plots)				
log1p(Biomass)	1	0.1529	1.4946	0.017
Stand age	1	1.1520	1.4854	0.023
Residual	45	4.6044		

Abbreviations: **Df** – the degrees of freedom; **χ^2** – Chi-squared statistics; **F** – F-statistics; **Pr(>F)** – p-values.

on nutrient-poor sites, *Vaccinium myrtillus*, *P. sylvestris*, and *Melampyrum pratense* were isolated on all graphs (Fig. 3a, e). On nutrient-rich sites, *P. serotina*, *G. robertianum*, *P. padus*, *M. trinervia*, and *Alliaria petiolata* increased their cover with an increase in *P. serotina* biomass (Fig. 3f). In summer, we found statistically significant relationships between species composition and invader biomass in all studied cases ($p < 0.01$; **T**able 1). On nutrient-poor sites, species like *Rubus idaeus*, *R. fruticosus* agg., and *P. serotina* increased their cover with increasing *P. serotina* biomass (Fig. 3g). On nutrient-poor sites, species like *M. trinervia*, *F. convolvulus*, *Ch. majus*, *I. parviflora*, and *G. robertianum* increased their cover with an increase in *R. pseudoacacia* biomass (Fig. 3c). For control plots on nutrient-poor

sites, *V. myrtillus*, *P. sylvestris*, and *M. pratense* are isolated on all graphs (Fig. 3c, g). On nutrient-rich sites, *Dryopteris carthusiana*, *R. pseudoacacia*, *P. serotina*, *M. trinervia*, *Acer campestre*, and *A. platanoides* increased their cover with an increase in *R. pseudoacacia* biomass (Fig. 3d). On nutrient-rich sites, *P. padus*, *G. robertianum*, *P. serotina*, *Sambucus nigra*, and *M. trinervia* increased their cover with an increase in *P. serotina* biomass (Fig. 3h).

Indicator taxa for invasive tree biomass

In spring, we detected decliners and increasers only on nutrient-rich sites with *P. serotina* (Fig. 4a, b, e, f; T Suppl. material 1: tables S6–S13). The cover of *Agrostis capillaris* decreased while the cover of *Corylus avellana* increased with an increase in invader biomass (Fig. 4f). In summer, in nutrient-poor habitats with *P. serotina*, we found five increasers: *I. parviflora*, *R. idaeus*, *D. carthusiana*, *P. serotina*, and *Rubus fruticosus* agg., and no decliners (Fig. 4g). In nutrient-rich habitats with *P. serotina*, we found three decliners: *Pteridium aquilinum*, *Oxalis acetosella*, and *Q. petraea*, and two increasers: *P. padus* and *P. serotina* (Fig. 4h). In nutrient-poor habitats with *R. pseudoacacia*, we found four decliners (*V. myrtillus*, *M. pratense*, *P. sylvestris*, and *Q. petraea*) and nine increasers: *S. nigra*, *Ch. majus*, *I. parviflora*, *F. convolvulus*, *M. trinervia*, *G. robertianum*, *D. carthusiana*, *R. fruticosus* agg., and *R. pseudoacacia* (Fig. 4c). In nutrient-rich habitats with *R. pseudoacacia*, we found one decliner (*Q. petraea*) and five increasers: *Q. robur*, *C. avellana*, *D. carthusiana*, *R. pseudoacacia*, and *Ch. majus* (Fig. 4d).

Relationship between invasive tree biomass and understory alpha diversity

On nutrient-poor sites in spring, we found a negative relationship between *R. pseudoacacia* aboveground biomass and mean pairwise distance (decreased from 0.26 ± 0.12 to – 0.39 ± 0.19 along an increase in invader biomass from 0 to 116 Mg ha^{-1}). Along this gradient, we found an increase in functional dispersion (from -0.53 ± 0.16 to 0.41 ± 0.25), moisture EIV (4.9 ± 0.1 to 5.5 ± 0.1), soil reaction EIV (6.5 ± 0.4 to 3.9 ± 0.2), SLA CWM (206.1 ± 20.3 cm^2 g^{-1} to 323.7 ± 32.6 cm^2 g^{-1}), and maximum height CWM (2.11 ± 0.09 m to 4.68 ± 0.13 m). In summer we found a higher species richness (11.0 ± 0.1 species to 21.3 ± 0.1 species), Shannon's diversity index (0.98 ± 0.14 to 1.91 ± 0.19), moisture EIV (4.8 ± 0.1 to 5.4 ± 0.1), soil fertility EIV (3.7 ± 0.2 to 6.6 ± 0.3), soil reaction EIV (3.2 ± 0.3 to 6.7 ± 0.4), and SLA CWM (202.8 ± 0.1 cm^2 g^{-1} to 383.0 ± 0.1 cm^2 g^{-1}) in plots with higher *P. serotina* biomass (Figs 5, 6, Suppl. material 1: tables S14, S18).

On nutrient-rich sites in spring, we found a positive relationship between *R. pseudoacacia* aboveground biomass and Faith's phylogenetic diversity (increased from -0.52 ± 0.20 to 0.08 ± 0.25 along an increase in invader biomass from 0 to 208 Mg ha^{-1}). Along this gradient, we found an increase in mean pairwise distance (from -0.56 ± 0.23 to 0.18 ± 0.27). In summer we found a decrease in functional dispersion (from -0.32 ± 0.13 to -0.98 ± 0.19) and an increase in Faith's phylogenetic diversity (from -0.35 ± 0.20 to 0.34 ± 0.25) with increasing *R. pseudoacacia* biomass (Figs 5, 6, Suppl. material 1: tables S15, S19).

On nutrient-poor sites in spring, we found a positive relationship between *P. serotina* aboveground biomass functional dispersion (from -0.60 ± 0.17 to 0.07 ±

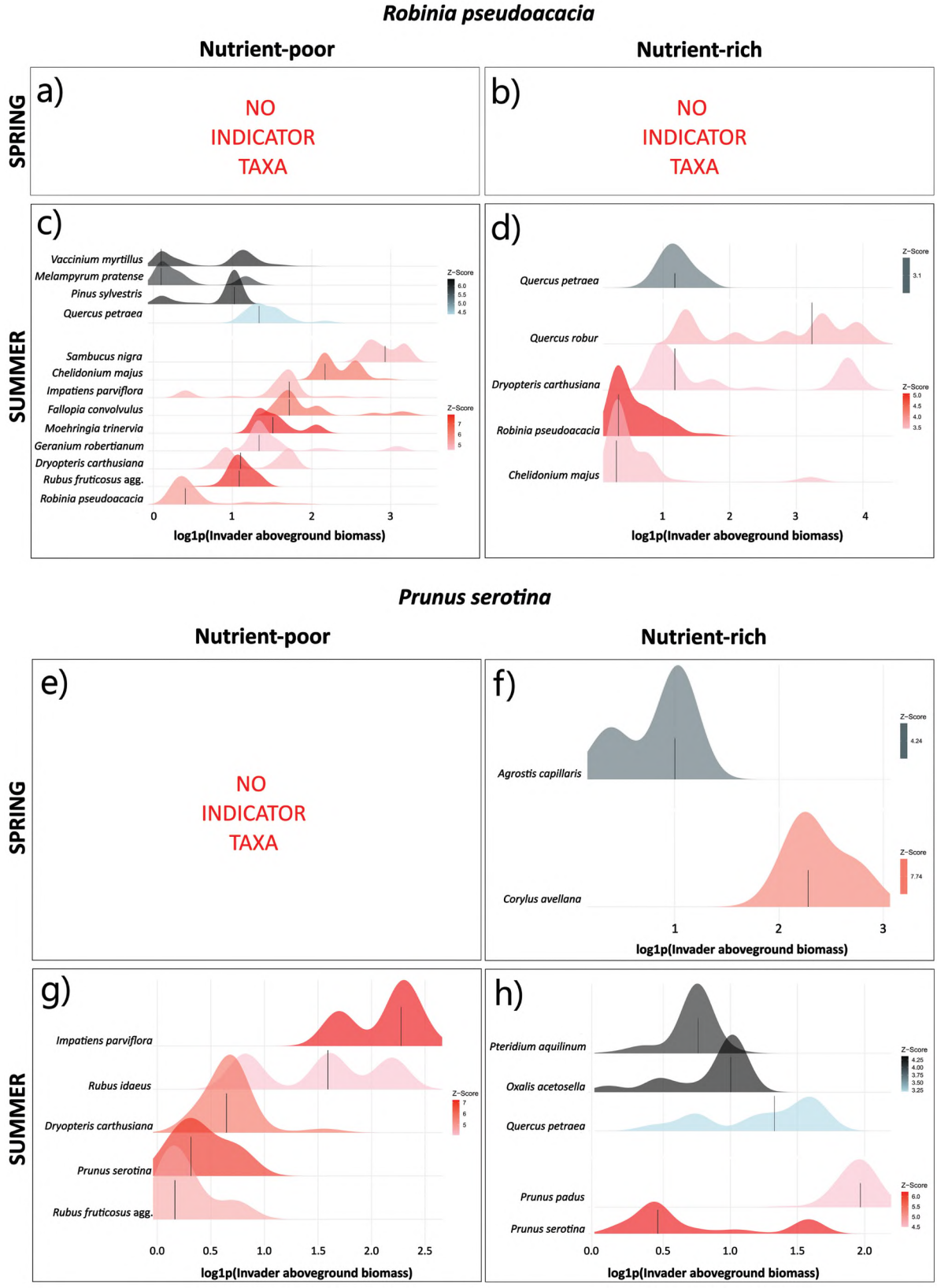

Figure 4. Results of the Threshold Indicator Taxa Analysis (see Methods section for graph interpretation) for all variants in both spring and summer: nutrient-poor sites with *P. serotina* (n = 47 plots), nutrient-rich sites with *P. serotina* (n = 48 plots), nutrient-poor sites with *R. pseudoacacia* (n = 48 plots), and nutrient-rich sites with *R. pseudoacacia* (n = 48 plots). Grey/light blue density estimators represent species responding negatively to the invader biomass gradient (decliners), while red color – positively (increasers). We included here only responses for species that were both reliable (reliability ≥ 0.95) and pure (purity ≥ 0.95). For statistics of all species, see Suppl. material 1: tables S6–S13.

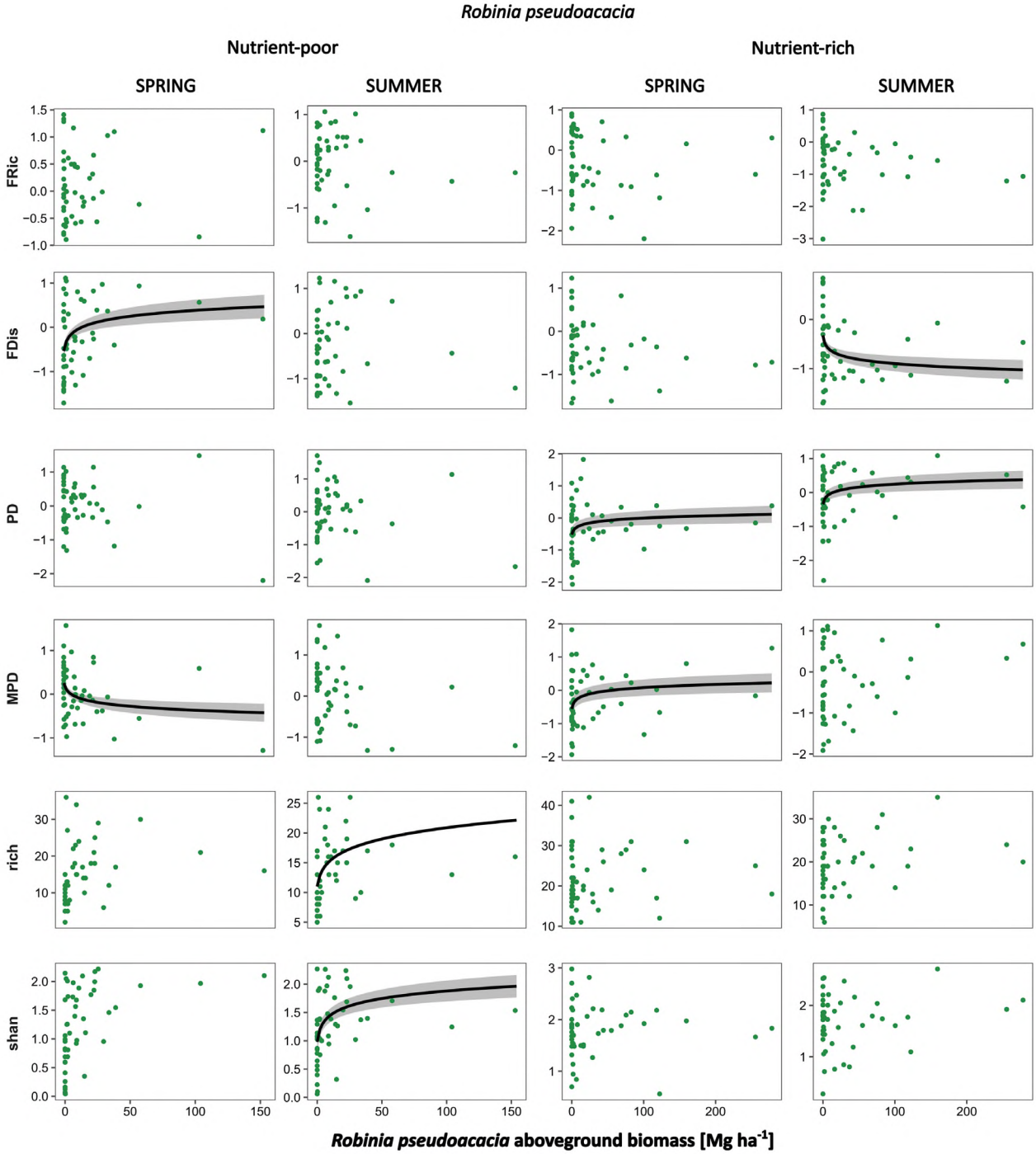

Figure 5. Generalized linear mixed-effect models for different plant diversity indicators depending on *Robinia pseudoacacia* aboveground biomass [Mg ha^{-1}] in both nutrient-poor and nutrient-rich sites in both spring and summer. Dark green dots – observed values; black line – marginal responses; grey area – marginal responses ± standard error. Marginal responses and marginal responses ± standard error only for statistically significant results. Abbreviations: **FRic** – SES Functional richness; **FDis** – SES Functional dispersion; **PD** – Faith's phylogenetic diversity; **MPD** – Mean Pairwise Distance; **rich** – Species richness; **shan** – Shannon's diversity index.

0.22) along with an increase in invader biomass from 0 to 16 Mg ha^{-1}. Along this gradient, we found an increase in species richness (from 9.6 ± 0.1 species to 13.7 ± 0.1 species), Shannon's diversity index (from 0.94 ± 0.22 to 1.43 ± 0.23), soil fertility EIV (from 3.6 ± 0.2 to 4.5 ± 0.3), soil reaction EIV increased (from 2.9 ± 0.3 to 4.9 ± 0.4), SLA CWM (from 197.2 ± 10.0 cm^2 g^{-1} to 240.6 ± 13.4 cm^2

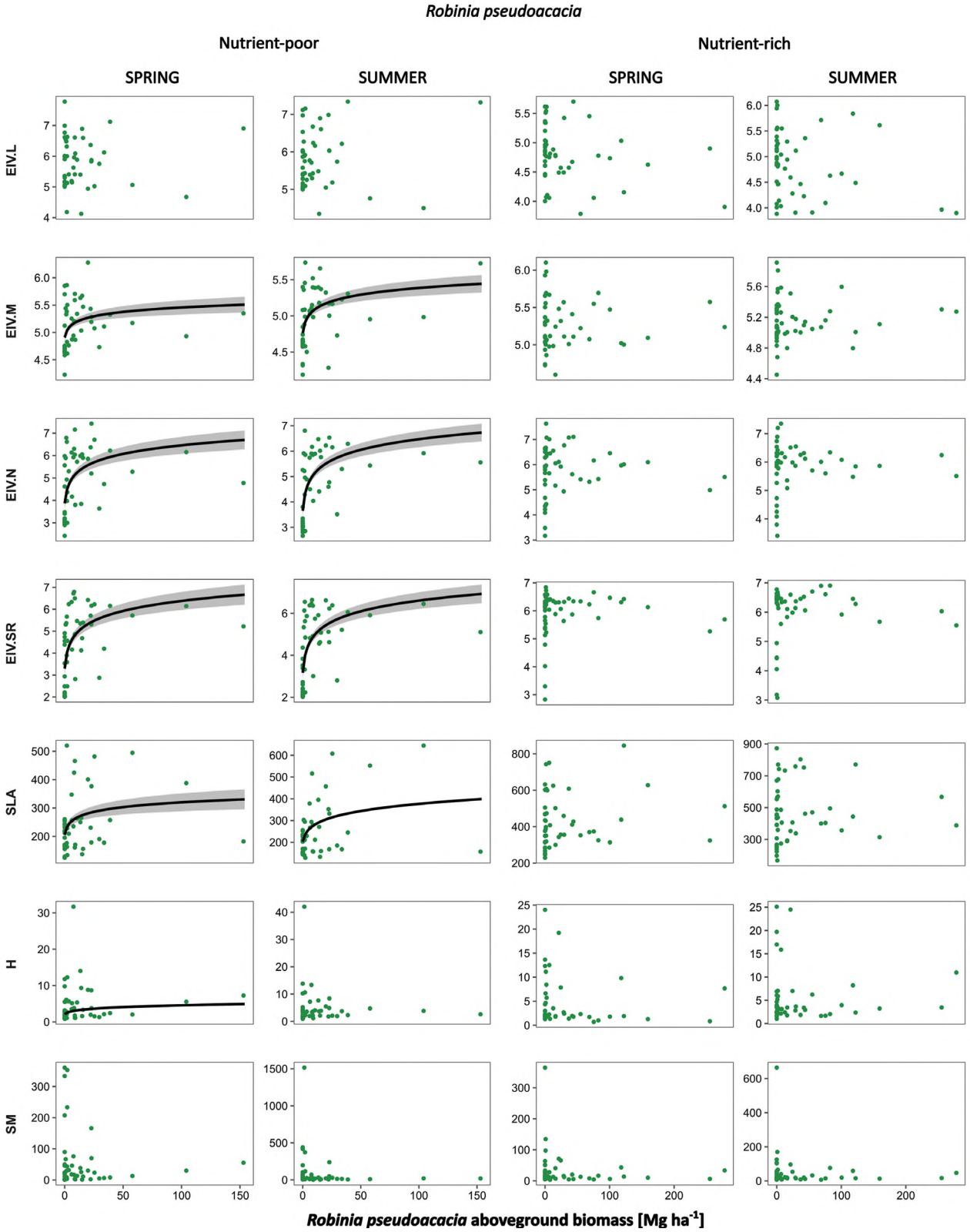

Figure 6. Generalized linear mixed-effect models for community-weighted means of functional traits and EIVs depending on *Robinia pseudoacacia* aboveground biomass [Mg ha^{-1}] in both nutrient-poor and nutrient-rich sites in both spring and summer. Dark green dots – observed values; black line – marginal responses; grey area – marginal responses ± standard error. Marginal responses and marginal responses ± standard error only for statistically significant results. Abbreviations: **EIV.L** – Light EIV; **EIV.M** – Moisture EIVe; **EIV.N** – Soil Fertility EIV; **EIV.SR** – Soil Reaction EIV; **SLA** – Specific Leaf Area CWM [cm^2 g^{-1}]; **H** – Maximum height CWM [m]; **SM** – Seed mass CWM [mg].

g^{-1}), and maximum height CWM (from 2.31 ± 0.07 m to 12.38 ± 0.09 m). In summer we found an increase in functional richness (from -0.02 ± 0.21 to 0.74 ± 0.23), species richness (from 9.9 ± 0.2 species to 14.0 ± 0.2 species), moisture EIV (from 4.7 ± 0.1 to 4.9 ± 0.1), soil fertility EIV (from 3.4 ± 0.2 to 4.6 ± 0.2), soil reaction EIV (from 2.9 ± 0.3 to 4.9 ± 0.3), and maximum height CWM (from 2.85 ± 0.11 m to 10.12 ± 0.11 m) with increasing invader biomass (Figs 7, 8, Suppl. material 1: tables S16, S20).

On nutrient-rich sites in spring, we found a positive relationship between *P. serotina* aboveground biomass and soil reaction EIV (increased from 5.5 ± 0.2 to 6.3 ± 0.3 along an increase in invader biomass from 0 to 28 Mg ha^{-1}). Along this gradient, we found an increase in maximum height CWM (from 2.79 ± 0.07 m to 6.79 ± 0.11 m) and SLA CWM (from 354.7 ± 25.7 cm^2 g^{-1} to 522.5 ± 42.4 cm^2 g^{-1}), with an increase in invader biomass. On nutrient-rich sites in summer, we did not find any statistically significant relationship between studied plant alpha diversity indicators, EIVs, and CWM of functional traits and *P. serotina* biomass (Figs 7, 8, Suppl. material 1: tables S17, S21).

Discussion

General patterns and species-specific trends

We confirmed the first and second hypotheses, revealing different relationships between alpha diversity and invader biomass for both studied neophytes. We found an overall increase in functional dispersion, species richness, and Shannon's index for both studied species in nutrient-poor sites, and an increase in phylogenetic diversity with increasing *R. pseudoacacia* biomass in nutrient-rich sites. Additionally, on nutrient-poor sites, we found an increase in functional richness for increasing biomass of *P. serotina* and a decrease in the mean pairwise distance for increasing biomass of *R. pseudoacacia*.

The relationship between invader biomass depended on particular diversity indices. We observed different indicator species for those two neophytes. In all CCA ordinations (Fig. 3) on nutrient-poor sites, we observed that these species were always associated with non-invaded plots: *V. myrtillus*, *P. sylvestris*, and *M. pratense*. These species are very important for natural coniferous forest communities in Central Europe, typical of *Dicrano-Pinion* W. Mat. 1962 alliance (Matuszkiewicz 2001). However, TITAN2 analysis confirms this negative relationship between invaders and these species only for nutrient-poor sites with *R. pseudoacacia* in summer (Fig. 4). *Vaccinium myrtillus*, *P. sylvestris*, and *M. pratense* prefer acidic soils, so their decreasing cover along the invader biomass can be caused by increasing soil pH and fertility, expressed by the increase in EIVs (Figs 6, 8). Also, Halarewicz and Pruchniewicz (2015) found a decrease in the frequency of the same species that, in our study, an increase in *P. serotina* cover, on nutrient-poor sites. A previous study (Woziwoda et al. 2021) confirmed the negative effect of invasive *Quercus rubra* presence on *V. myrtillus* cover in Scots pine forests, attributing this impact to decreasing light availability. This was in line with our observations. *Robinia pseudoacacia*, as a species with the ability to fix nitrogen, supplies large amounts of nitrogen into the soil (Danso et al. 1995; Noh et al. 2010), affecting species composition (Rice et al. 2004). This is in line with our observation of nitrophilous species such as *I. parviflora*, *G. robertianum*, or *M. trinervia*, where we observed

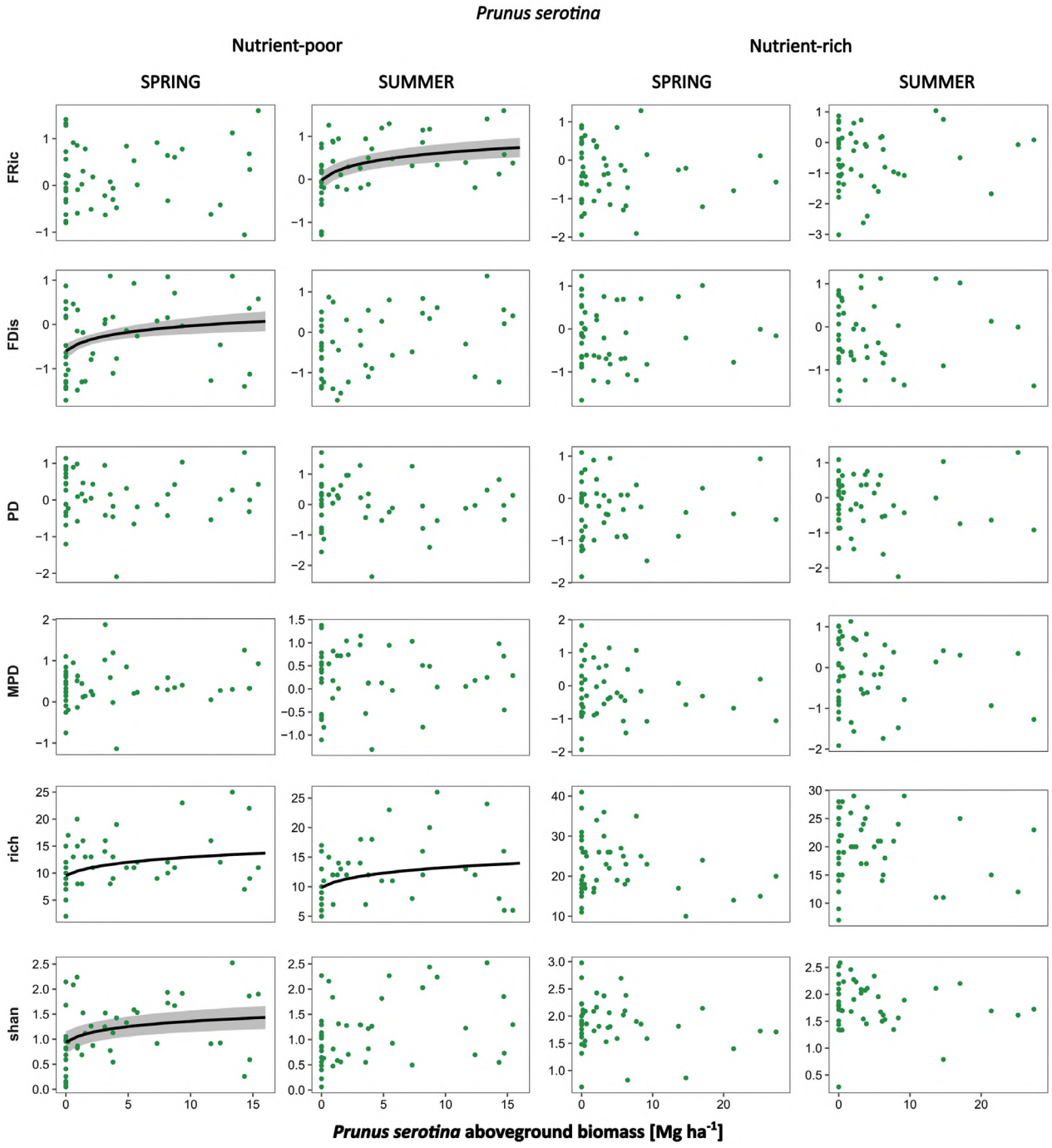

Figure 7. Generalized linear mixed-effect models for different plant diversity indicators depending on *Prunus serotina* aboveground biomass [Mg ha^{-1}] in both nutrient-poor and nutrient-rich sites in both spring and summer. Dark green dots – observed values; black line – marginal responses; grey area – marginal responses ± standard error. Marginal responses and marginal responses ± standard error only for statistically significant results. Abbreviations: **FRic** – SES Functional richness; **FDis** – SES Functional dispersion; **PD** – Faith's phylogenetic diversity; **MPD** – Mean Pairwise Distance; **rich** – Species richness; **shan** – Shannon's diversity index.

a positive relationship between their cover and invader biomass. These species are known to respond positively to nitrogen deposition (Perring et al. 2018). Similarly, Halarewicz and Pruchniewicz (2015) found an increase in *I. parviflora* frequency with increasing *P. serotina* cover. Despite a different nitrogen management strategy than *R. pseudoacacia*, *P. serotina* also supplies a large amount of this element into the soil (Aerts et al. 2017; Horodecki et al. 2019).

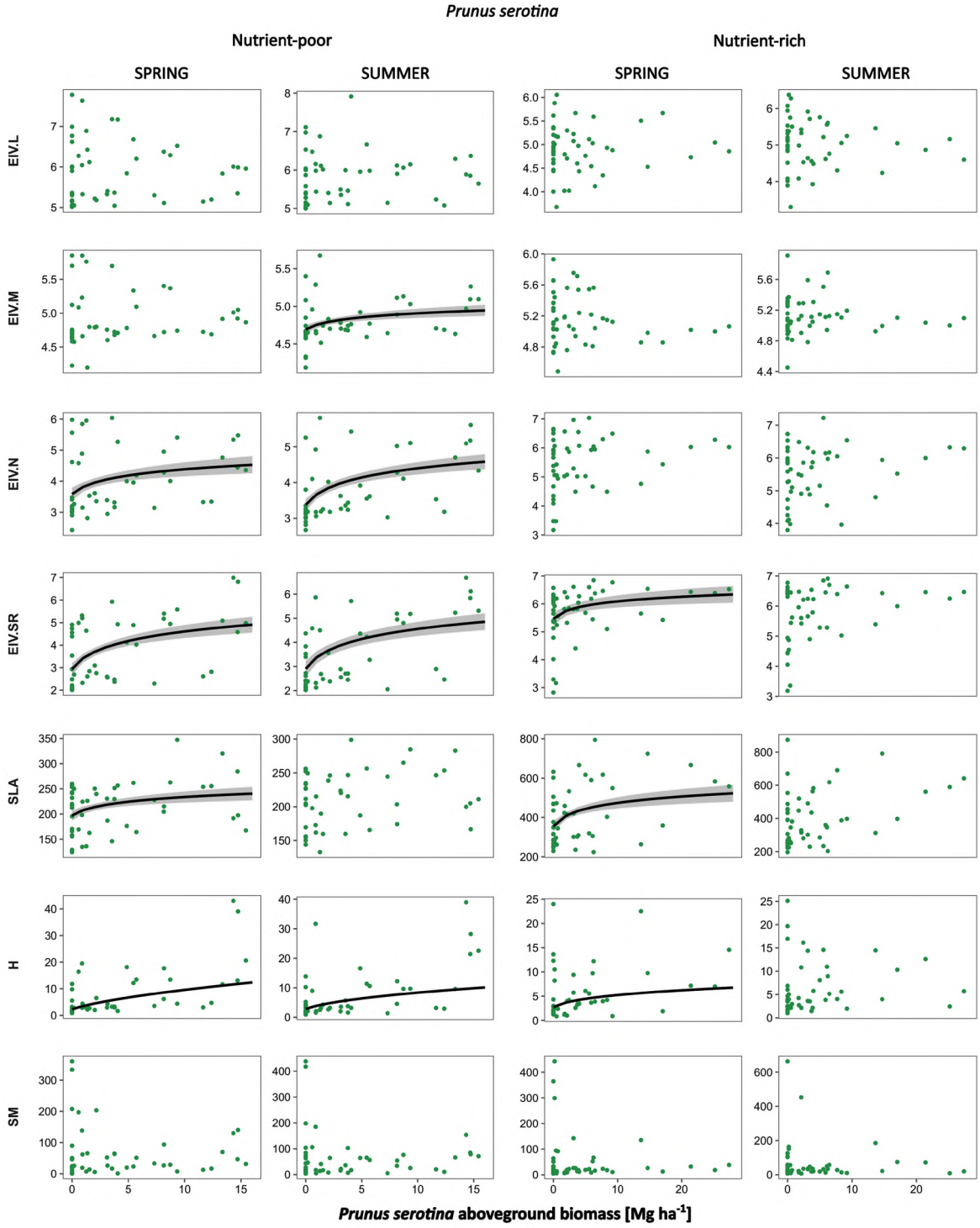

Figure 8. Generalized linear mixed-effect models for community-weighted means of functional traits and EIVs depending on *Prunus serotina* aboveground biomass [Mg ha^{-1}] in both nutrient-poor and nutrient-rich sites in both spring and summer. Dark green dots – observed values; black line – marginal responses; grey area – marginal responses ± standard error. Marginal responses and marginal responses ± standard error only for statistically significant results. Abbreviations: **EIV.L** – Light EIV; **EIV.M** – Moisture EIV; **EIV.N** – Soil Fertility EIV; **EIV.SR** – Soil Reaction EIV; **SLA** – Specific Leaf Area CWM [cm^2 g^{-1}]; **H** – Maximum height CWM [m]; **SM** – Seed mass CWM [mg].

Previous studies about both *P. serotina* (Chabrerie et al. 2008, 2010) and *R. pseudoacacia* (Montecchiari et al. 2020) per capita effect on understory biodiversity focused on the cover as an abundance metric. Chabrerie et al. (2010), examining the overstory dominance of *P. serotina*, showed that more specialized species were in

invaded stands, and the species richness and vegetation cover were lower, in contrast to our study. Traits describing shade tolerance, ruderal plants with a short life cycle, and geophytes were associated with invaded habitats, and light-demanding species were associated with non-invaded stands. Chabrerie et al. (2008) showed that the communities of herbaceous species differed slightly between those with *P. serotina* and those without. The trend observed in Chabrerie et al. (2008) is therefore opposite to ours. In our study, true forest species were more associated with areas with lower invader biomass, and with the increasing amount of invader biomass, the coverage of ruderal and edge species increased (e.g., *Rubus* spp. in nutrient-poor habitats invaded by *P. serotina*, *I. parviflora*, *G. robertianum*, or *M. trinervia* in nutrient-poor habitats invaded by *R. pseudoacacia*), while forest specialists decreased (e.g., *P. sylvestris* and *V. myrtillus* in nutrient-poor habitats with *R. pseudoacacia*). These differences may result from local environmental conditions and different species compositions of stands. In our study, we had either pine or oak stands. Chabrerie et al. (2008) assessed mixed stands with beech, oak, and pine in a single large forest complex (14,417 ha). Our plots were in various scattered forest complexes, from very small (approx. 12 ha) to large, compact complexes (approx. 15,000 ha–Zielonka Forest). In contrast to our results, Montecchiari et al. (2020) confirm that *R. pseudoacacia* increasing cover increased the presence of alien species and nitrophilous species and decreased Shannon's diversity index in *Quercus pubescens* sub-Mediterranean forests. Šibíková et al. (2019) showed that in the invaded stands dominated by *R. pseudoacacia*, there were more common generalists, and the pool of species decreased from 442 to 372 species compared to the native nutrient-rich (oak forests, oak-hornbeam forests, and hardwood floodplain forests) forests. For *R. pseudoacacia* stands, they found many nitrophilous species, e.g., *Ch. majus*, *S. nigra*, *Geum urbanum*, and heliophilous grasses, e.g., *Arrhenatherum elatius*, similarly to our study. Slabejová et al. (2023) showed that stands invaded by *R. pseudoacacia* were characterized by greater availability of light on the forest floor, higher temperature, and lower humidity. In the understory, increasing coverage of ruderal, non-forest species and a greater share of alien species were observed in comparison to native stands. However, native stands differed in terms of changes caused by the replacement by *R. pseudoacacia*. Floodplain forests were less affected than mixed oak-hornbeam forests. As floodplain forests are more fertile than oak-hornbeam forests, this trend is in line with our results, indicating higher resistance of nutrient-rich habitats.

Context dependence and biotic resistance

Previous studies confirmed differences between nutrient-poor and nutrient-rich habitats in relationships between invasive trees and plant diversity (H3). They revealed both positive (Von Holle et al. 2013; Gentili et al. 2019; Bury and Dyderski 2024a) and negative (Godefroid et al. 2005; Trentanovi et al. 2013; Lazzaro et al. 2018; Gentili et al. 2019; Kowarik et al. 2019; Montecchiari et al. 2020) effects of studied invaders on taxonomic alpha diversity, while most of them showed insignificant relationships (e.g., Verheyen et al. 2007; Hejda et al. 2017; Sitzia et al. 2018; Gentili et al. 2019; Slabejová et al. 2019). However, most of them focused on nutrient-rich sites. Only five focused on nutrient-poor sites (Verheyen et al. 2007; Halarewicz 2012; Halarewicz and Żołnierz 2014; Dyderski and Jagodziński 2021; Bury and Dyderski 2024a). In our study, the increase in taxonomic diversity was statistically significant only in the nutrient-poor sites (Figs 5, 7). However,

the number of species does not describe the quality of species composition. In our study, in nutrient-poor habitats, the relationships between invader biomass and the CWMs of EIV.M, EIV.N, and EIV.SR increased with invader biomass increase (Figs 6, 8). These results might indicate transformations of case soil characteristics by invaders (Danso et al. 1995; Noh et al. 2010; Aerts et al. 2017; Kato-Noguchi and Kato 2024). This may be related to the emergence of species that prefer more fertile and alkaline soils and may promote forest generalists, leading to the decline of forest specialists (Woziwoda et al. 2014, 2019; Slabejová et al. 2019; Šibíková et al. 2019). The decrease and increase in species cover are reflected in differences in the individual alpha diversity indices of each type.

In nutrient-poor habitats, FDis increases with increasing invader biomass. In the nutrient-rich habitats, on the other hand, for summer, FDis decreased for *R. pseudoacacia* (Fig. 5). The observed increase in functional diversity for *R. pseudoacacia* can be explained by the expansion of ruderal, edge, and nitrophilous species in sites dominated by acidophilous species. That way, invaded communities comprise species from both groups, enriching the set of functional traits and their diversity. This condition is caused by the enrichment of soil in a nutrient-rich leaf litter (Rice et al. 2004; Horodecki et al. 2019) of *R. pseudoacacia*, which increases soil pH and fertility. The same processes can explain the increase in FDis in nutrient-poor habitats with *P. serotina*.

The decline in the mentioned functional diversity indicators in a nutrient-rich habitat is slightly more difficult to interpret. These habitats are naturally characterized by higher diversity. The changes in EIVs caused by the presence of *R. pseudoacacia* on nutrient-rich sites were statistically insignificant. In our previous study, conducted in Wielkopolska National Park, about the per capita effect (based on aboveground biomass proportion of *P. serotina* in total biomass) of *P. serotina* invasion on understory alpha diversity, we found a positive relationship between total species richness (+ 8.8 species) and functional richness (+ 0.08) along proportion of *P. serotina* in stand biomass ranging from 0 to 10%. However, we investigated this relationship in natural *P. sylvestris* stands and nutrient-rich sites with artificially planted *P. sylvestris*. In this study we noticed that light played a significant role as a driver of changes, and both the understory plants and the *P. serotina* itself benefited from the higher availability of light. Dyderski and Jagodziński (2021) showed that *P. sylvestris* plantations (on fertile soils) invaded by *P. serotina* have one-fourth higher species richness than non-invaded ones, and non-invaded *P. sylvestris* stands (on nutrient-poor soils) had 13% more species than those invaded by *P. serotina*, while *Quercus-Acer-Tilia* stands (similar to our control stands on nutrient-rich sites) had 15% lower species richness than *R. pseudoacacia* stands. Thus, in a previous study, we found higher functional alpha diversity in *P. sylvestris* stands invaded by *P. serotina* than in non-invaded stands and higher in *R. pseudoacacia* stands than in *Quercus-Acer-Tilia* stands (Dyderski and Jagodziński 2021).

The increase in both MPD and PD in the forest habitat with *R. pseudoacacia* suggests that the number of evolutionary pathways, expressed by tree branches, is higher in more invaded sites. This may result from the fact that emerging species are more diverse in terms of phylogeny than the plants present in the ecosystem before invasion. In turn, the decreasing number of forest specialists in nutrient-poor habitats with *R. pseudoacacia*, representing different clades, e.g., *V. myrtillus* and *M. pratense*, or *P. sylvestris*, with the simultaneous introduction of nitrophilous generalists with closer phylogeny might lead to a decrease in MPD. These differences between nutrient-rich and nutrient-poor habitats can be explained by Piwczyński et al.'s (2016)

study. They proved that different alien species can shape the relationship between phylogenetic variability and the presence of an alien species in different ways. Additionally, the authors proved that environmental conditions, i.e., soil pH and light availability, were more important in shaping phylogenetic diversity than dominant tree species. This explains why we observed a different reaction in the nutrient-poor and forest habitats where the transformations of conditions were stronger, which is reflected in the significant results for EIVs. The mechanisms responsible for the species composition of the community can be explained by their phylogenetic structure. Environmental filtering, i.e., when species with similar ecological features can survive in unfavorable conditions, can lead to phylogenetic attraction. On the other hand, phylogenetic overdispersion indicates the dominant importance of interspecific competition. In such a situation, phylogenetically distinct species with different ecological features dominate in a given community. Our study plots were characterized by different intensities of invasion. In the early phases of invasion, characterized by greater environmental instability, we observed the advantage of clustering associated with the action of environmental filtration. In the later stages of invasion, stability increases and interspecific competition increases at the same time, leading to phylogenetic overdispersion (Webb et al. 2002). Other authors confirm that the phylogenetic structure of communities can change along the environmental gradient (Webb and Peart 2000; Cavender-Bares and Holbrook 2001). Our previous studies are in line with new results: Dyderski and Jagodziński (2021) found a higher phylogenetic diversity in *P. sylvestris* stands invaded by *P. serotina* than in non-invaded stands. The phylogenetic diversity was higher in *R. pseudoacacia* stands than in control *Quercus-Acer-Tilia* stands. Confirming the same trends using a quantitative gradient of invasive tree abundance in managed forests highlights the generality of discovered patterns. However, previous studies focused more on taxonomic and functional diversity, not allowing us a wider comparison of these trends.

Seasonality

Our results partially supported the fourth hypothesis. In spring we found species related to invader biomass gradient only on nutrient-rich sites with *P. serotina* (two species), with no indicator species in other variants. We expected that the presence of *R. pseudoacacia* and *P. serotina*, especially *R. pseudoacacia* in the overstory in nutrient-rich habitats, would significantly affect spring species. Compared to native oaks, *R. pseudoacacia* transmits more light through to the forest floor (Slabejová et al. 2019, 2023) and also develops foliage later than native oaks. This could create favorable conditions for the development of geophytes–a group of plants that are an important element of the species composition in spring in oak-hornbeam forests (Rawlik et al. 2023). Perhaps due to their ephemeral nature, these plants are less threatened by disturbances related to the presence and transformation of invasive species, because changes in soil chemistry are not so significant in fertile habitats. What is more interesting, according to our results, is that in both summer and spring (for *R. pseudoacacia*), the light EIV (Fig. 6) suggests better conditions for shade-tolerant species. In turn, in summer there were many more of these species. Some of the species were present in both seasons; however, there were differences in their cover, especially of the geophytes. In spring, some understory species have already started to grow, so their cover is low. Therefore, it is difficult to clearly state to what extent the lack of indicator species depends on the actual relationship of invaders with the understory, or whether in general the statis-

tical power of analyses based on the spring dataset is too low. Comparing spring and summer responses, observed on CCA graphs (Fig. 3), we can find that *M. trinervia*, *F. convolvulus*, *Ch. majus*, *I. parviflora*, *R. pseudoacacia*, and *G. robertianum* are typical of sites with higher *R. pseudoacacia* biomass. This may indicate the high population stability of these species in nutrient-poor habitats with *R. pseudoacacia*. *Fallopia convolvulus*, *Ch. majus*, and *I. parviflora* are nitrophilous, ruderal species, peculiar to habitats transformed by different human activities, while *M. trinervia* is an edge species more typical for forest edges (Ratyńska et al. 2010; Mucina et al. 2016). The same trend (according to CCA spring vs. summer) was observed for stands with *P. serotina* for *R. idaeus*, *R. fruticosus* agg., and *P. serotina*. We obtained very similar results comparing spring and summer for species richness (increase; Fig. 5) for *P. serotina* on nutrient-poor habitats and PD (increase; Fig. 7) for *R. pseudoacacia* on nutrient-rich habitats (Fig. 5). It is difficult to determine what accounts for the consistency or divergence between individual indicators for spring and summer. It may be related to the presence or absence of tree leaves in particular seasons (Heinrich 1976; Kudo et al. 2008; Rawlik et al. 2023). There may be a difference between spring and summer in the context of resource use by plants and seasonal differences in resource availability (Tonkin et al. 2017; Yan et al. 2023). It can determine the impact or lack of impact in spring or summer, and individual alpha diversity indices are characterized by different stability, e.g., the total number of species will change, but their functional features or phylogeny are not significantly different from those of species present before the invasion. However, seasonality in the context of studying the impact of tree invasions, especially scaled effects, on the understory is not well understood.

Forest understory vegetation conservation and invasive tree management

The potential effect of ecosystem transformations of *P. serotina* and *R. pseudoacacia* seems to be more visible and stronger in nutrient-poor habitats. This is important in the context of protecting habitats for acidophilous plants. Our study shows that the relationship between acidophilous species cover and invader biomass is negative. Of course, we studied semi-natural managed forests. However, if we apply the above premise to valuable, protected forests, we may fear that acidophilous, protected, and rare species may also poorly tolerate the growing biomass of *R. pseudoacacia* and *P. serotina*. Our study showed that it is very important to look deeper into biodiversity, not only focusing on numbers–total species richness–but also on species structure–particular species abundance–in particular habitat types and seasons. *Vaccinium myrtillus* is a very important component of nutrient-poor forest vegetation in Central and Northern Europe (Ritchie 1956). A serious question that can be asked based on our results is whether the sacrifice of dominant species important for coniferous habitats can be sacrificed in the name of increasing species richness. Perhaps more studies are needed to assess even more precisely in what configurations this wealth will decrease. A better assessment of the scaled effect at higher levels of diversity, e.g., gamma biodiversity, is also needed. Changes in nutrient-rich habitats are less intensive than in the case of nutrient-poor habitats. This is consistent with previous works by various authors (Chmura 2004; Halarewicz 2011; Bury and Dyderski 2025a, b). In these habitats, maintaining and improving the resistance of native habitats is crucial. This can be achieved by supporting the addition of native tree species that tolerate competition from the studied invasive species

(Nyssen and Vanhellemont 2016; Sádlo et al. 2017). There are various methods of preventing and combating invasive tree species. Unfortunately, sometimes the eradication of invasive trees can complicate management (Namura-Ochalska and Borowa 2015; Nyssen et al. 2024). For both *P. serotina* (Nyssen and Vanhellemont 2016) and *R. pseudoacacia* (Sádlo et al. 2017), management should be specific to the habitat and protection status of a given forest area (Nyssen and Vanhellemont 2016; Sádlo et al. 2017). As Sádlo et al. (2017) emphasize for *R. pseudoacacia*, various stakeholders should be reconciled to reach a compromise between different ecological and economic values. Increasing resistance might include decreasing forest patch invasibility by maintaining a closed canopy or decreasing propagule pressure by eliminating reproducing specimens of invasive trees in the surroundings.

Conclusion

We confirmed that the impacts of two invasive species, *P. serotina* and *R. pseudoacacia*, on species composition and alpha diversity of the understory scale with invader biomass. We also showed differences in impacts between habitats and seasons. We found various spring and summer indicator species for *P. serotina* and *R. pseudoacacia* quantity in nutrient-poor habitats dominated by *P. sylvestris* and nutrient-rich habitats dominated by *Q. petraea*/*robur*. Additionally, we showed that *P. serotina* and *R. pseudoacacia* had different relationships between their biomass and various indicators of taxonomic, functional, and phylogenetic diversity in particular habitats and seasons. Especially on nutrient-poor sites, we can see that ruderal and forest edge species increased their cover with invader biomass increasing, while forest specialists typical for those habitats decreased their cover. Due to the protection of natural habitats for acidophilous plants, the decreasing coverage of specialists, more noticeable for stands with *R. pseudoacacia* in our study, is worrying. These results confirm that we should focus more attention on nutrient-poor habitats and increase the resistance of these stands to invasion, and this should apply to stands with different functions and different protection regimes. Our results draw attention to the complex issue of the presence of invasive trees in forest ecosystems, and we proved that the relationship between invader biomass and understory vegetation is context-dependent. Field observations, their analysis, and their interpretation enrich our knowledge and should contribute to better management of invasive tree species and better protection of semi-natural and natural ecosystems. It is worth examining biodiversity at many levels and examining the impact of invasive trees in different habitats and seasons. It is also important to study not only the presence or absence of invaders but also the effect on their biomass.

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Additional information

Conflict of interest

The authors declare no conflict of interest. The funders had no role in the design of the study; in the collection, analyses, or interpretation of data; in the writing of the manuscript; or in the decision to publish the results.

Ethical statement

The study did involve human or animal participants as study subjects. Authors obtained consent for fieldwork from the respective State Forest Districts.

Use of AI

Authors declare that AI was not used for the research and manuscript preparation.

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Author contributions

Conceptualization: SB, MKD; methodology: SB, MKD; investigation: SB, MKD; formal analysis: SB; visualization: SB; writing–original draft preparation: SB; writing–review and editing: MKD; funding acquisition: MKD.

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Data availability

All data supporting the results are archived in the Figshare repository (10.6084/m9.figshare.28494962). For review purposes, please use the following link: https://figshare.com/s/8de871c9063c8ff4b600.

References

Aerts R, Ewald M, Nicolas M, Piat J, Skowronek S, Lenoir J, Hattab T, Garzón-López CX, Feilhauer H, Schmidtlein S, Rocchini D, Decocq G, Somers B, Van De Kerchove R, Denef K, Honnay O (2017) Invasion by the Alien Tree *Prunus serotina* Alters Ecosystem Functions in a Temperate Deciduous Forest. Frontiers in Plant Science 8. https://doi.org/10.3389/fpls.2017.00179

Alberti G, Candido P, Peressotti A, Turco S, Piussi P, Zerbi G (2005) Aboveground biomass relationships for mixed ash (*Fraxinus excelsior* L. and *Ulmus glabra* Hudson) stands in Eastern Prealps of Friuli Venezia Giulia (Italy). Annals of Forest Science 62: 831–836. https://doi.org/10.1051/forest:2005089

Baker M, King R, Kahle D (2023) TITAN2: Threshold Indicator Taxa Analysis. R package version 2.4.3. https://CRAN.R-project.org/package=TITAN2

Bartoń K (2017) MuMIn: Multi-Model Inference. https://cran.r-project.org/web/packages/MuMIn/index.html

BDL (2024) Bank Danych o Lasach. https://www.bdl.lasy.gov.pl/portal/mapy-en [Accessed 06 August 2024]

Benesperi R, Giuliani C, Zanetti S, Gennai M, Mariotti Lippi M, Guidi T, Nascimbene J, Foggi B (2012) Forest plant diversity is threatened by *Robinia pseudoacacia* (black-locust) invasion. Biodiversity and Conservation 21: 3555–3568. https://doi.org/10.1007/s10531-012-0380-5

Bouteiller XP, Bussolo M, Ségura R, Mariette S, Porté AJ (2023) Considering both sexual and clonal reproduction could help loosen the conflict of use over *Robinia pseudoacacia*. Dendrobiology 90: 30–38. https://doi.org/10.12657/denbio.090.002

Brondízio ES, Settele J, Díaz S, Ngo HT [Eds] (2019) The global assessment report of the intergovernmental science-policy platform on biodiversity and ecosystem services. Intergovernmental Science-Policy Platform on Biodiversity and Ecosystem Services (IPBES), Bonn.

Brooks ME, Kristensen K, van Benthem KJ, Magnusson A, Berg CW, Nielsen A, Skaug HJ, Maechler M, Bolker BM (2017) glmmTMB Balances Speed and Flexibility Among Packages for Zero-inflated Generalized Linear Mixed Modeling. The R Journal 9(2): 378–400. https://doi.org/10.32614/RJ-2017-066

Brown JK (1976) Estimating shrub biomass from basal stem diameters. Canadian Journal of Forest Research 6(2): 153–158. https://doi.org/10.1139/x76-019

Brus R, Pötzelsberger E, Lapin K, Brundu G, Orazio C, Straigyte L, Hasenauer H (2019) Extent, distribution and origin of non-native forest tree species in Europe. Scandinavian Journal of Forest Research 34: 533–544. https://doi.org/10.1080/02827581.2019.1676464

Buckley HL, Hall D, Jarvis RM, Smith V, Walker LA, Silby J, Hinchliffe G, Stanley MC, Sweeney AP, Case BS (2023) Using long-term experimental restoration of agroecosystems in Aotearoa New Zealand to improve implementation of Nature-based Solutions for climate change mitigation. Frontiers in Forests and Global Change 5: e950041. https://doi.org/10.3389/ffgc.2022.950041

Bury S, Dyderski MK (2024a) In search of *per capita* effects of *Prunus serotina* Ehrh. invasion on temperate forest understory alpha diversity. Biologia 79: 3011–3025. https://doi.org/10.1007/s11756-024-01766-7

Bury S, Dyderski MK (2024b) No effect of invasive tree species on aboveground biomass increments of oaks and pines in temperate forests. Forest Ecosystems 11: e100201. https://doi.org/10.1016/j.fecs.2024.100201

Bury S, Dyderski MK (2025a) Invasive *Prunus serotina* vs. *Robinia pseudoacacia*: How does temperate forest natural regeneration respond to their quantity? NeoBiota 97: 179–213. https://doi.org/10.3897/neobiota.97.135421

Bury S, Dyderski MK (2025b) Invasive tree species affect terricolous bryophytes biomass and biodiversity in nutrient-poor but not nutrient-rich temperate forests. Scientific Reports 15: e5272. https://doi.org/10.1038/s41598-025-89917-x

Cavender-Bares J, Holbrook NM (2001) Hydraulic properties and freezing-induced cavitation in sympatric evergreen and deciduous oaks with contrasting habitats. Plant, Cell & Environment 24: 1243–1256. https://doi.org/10.1046/j.1365-3040.2001.00797.x

Chabrerie O, Verheyen K, Saguez R, Decocq G (2008) Disentangling relationships between habitat conditions, disturbance history, plant diversity, and American black cherry (*Prunus serotina* Ehrh.) invasion in a European temperate forest: Invasion-disturbance-ecosystem interactions. Diversity & Distributions 14: 204–212. https://doi.org/10.1111/j.1472-4642.2007.00453.x

Chabrerie O, Loinard J, Perrin S, Saguez R, Decocq G (2010) Impact of *Prunus serotina* invasion on understory functional diversity in a European temperate forest. Biological Invasions 12: 1891–1907. https://doi.org/10.1007/s10530-009-9599-9

Chmura D (2004) Penetration and naturalisation of invasive alien plant species (neophytes) in woodlands of the Silesian Upland (Southern Poland). Nature Conservation 60: 3–11.

Cierjacks A, Kowarik I, Joshi J, Hempel S, Ristow M, Von Der Lippe M, Weber E (2013) Biological Flora of the British Isles: *Robinia pseudoacacia*. Journal of Ecology 101: 1623–1640. https://doi.org/10.1111/1365-2745.12162

Closset-Kopp D, Chabrerie O, Valentin B, Delachapelle H, Decocq G (2007) When Oskar meets Alice: Does a lack of trade-off in r/K-strategies make *Prunus serotina* a successful invader of European forests? Forest Ecology and Management 247: 120–130. https://doi.org/10.1016/j.foreco.2007.04.023

Conradi T, Van Meerbeek K, Ordonez A, Svenning J (2020) Biogeographic historical legacies in the net primary productivity of Northern Hemisphere forests. Ecology Letters 23: 800–810. https://doi.org/10.1111/ele.13481

Corenblit D, Steiger J, Tabacchi E, González E, Planty-Tabacchi A-M (2014) Ecosystem engineers modulate exotic invasions in riparian plant communities by modifying hydrogeomorphic

connectivity: Ecosystem engineers modulate exotic invasions. River Research and Applications 30: 45–59. https://doi.org/10.1002/rra.2618

Crooks JA (2002) Characterizing ecosystem-level consequences of biological invasions: The role of ecosystem engineers. Oikos 97: 153–166. https://doi.org/10.1034/j.1600-0706.2002.970201.x

Czapiewska N, Dyderski MK, Jagodziński AM (2019) Seasonal dynamics of floodplain forest understory–Impacts of degradation, light availability and temperature on biomass and species composition. Forests 10: 1–22. https://doi.org/10.3390/f10010022

Czortek P, Orczewska A, Dyderski MK (2021) Niche differentiation, competition or habitat filtering? Mechanisms explaining co-occurrence of plant species on wet meadows of high conservation value. Journal of Vegetation Science 32: e12983. https://doi.org/10.1111/jvs.12983

Danso SKA, Zapata F, Awonaike KO (1995) Measurement of biological N_2-fixation in field-grown *Robinia pseudoacacia* L. Soil Biology & Biochemistry 27: 415–419. https://doi.org/10.1016/0038-0717(95)98612-R

Deckers B, Verheyen K, Vanhellemont M, Maddens E, Muys B, Hermy M (2008) Impact of avian frugivores on dispersal and recruitment of the invasive *Prunus serotina* in an agricultural landscape. Biological Invasions 10: 717–727. https://doi.org/10.1007/s10530-007-9164-3

Dickie IA, Yates GW, John MGSt, Stevenson BA, Scott JT, Rillig MC, Peltzer DA, Orwin KH, Kirschbaum MUF, Hunt JE, Burrows LE, Barbour MM, Aislabie J (2011) Ecosystem service and biodiversity trade-offs in two woody successions. Journal of Applied Ecology 48: 926–934. https://doi.org/10.1111/j.1365-2664.2011.01980.x

Diniz-Filho JAF, de Sant'Ana CER, Bini LM (1998) An eigenvector method for estimating phylogenetic inertia. Evolution; International Journal of Organic Evolution 52: 1247–1262. https://doi.org/10.1111/j.1558-5646.1998.tb02006.x

Dyderski MK, Jagodziński AM (2019) Similar Impacts of Alien and Native Tree Species on Understory Light Availability in a Temperate Forest. Forests 10: e951. https://doi.org/10.3390/f10110951

Dyderski MK, Jagodziński AM (2021) Impacts of invasive trees on alpha and beta diversity of temperate forest understories. Biological Invasions 23: 235–252. https://doi.org/10.1007/s10530-020-02367-6

Ellenberg H, Leuschner C (2010) Vegetation Mitteleuropas mit den Alpen in ökologischer, dynamischer und historischer Sicht. UTB, Stuttgart.

Engel M, Nyssen B, Desie E, Den Ouden J, Raats L, Hagemann U (2024) Managing Black Cherry (*Prunus serotina* Ehrh.) in European Forests: Insights from native and non-native ranges. Forest Ecology and Management 562: e121959. https://doi.org/10.1016/j.foreco.2024.121959

Felton A, Lindbladh M, Brunet J, Fritz Ö (2010) Replacing coniferous monocultures with mixed-species production stands: An assessment of the potential benefits for forest biodiversity in northern Europe. Forest Ecology and Management 260: 939–947. https://doi.org/10.1016/j.foreco.2010.06.011

Forrester DI, Tachauer IHH, Annighoefer P, Barbeito I, Pretzsch H, Ruiz-Peinado R, Stark H, Vacchiano G, Zlatanov T, Chakraborty T, Saha S, Sileshi GW (2017) Generalized biomass and leaf area allometric equations for European tree species incorporating stand structure, tree age and climate. Forest Ecology and Management 396: 160–175. https://doi.org/10.1016/j.foreco.2017.04.011

García RA, Fuentes-Lillo E, Cavieres L, Cóbar-Carranza AJ, Davis KT, Naour M, Núñez MA, Maxwell BD, Lembrechts JJ, Pauchard A (2023) *Pinus contorta* Alters Microenvironmental Conditions and Reduces Plant Diversity in Patagonian Ecosystems. Diversity 15. https://doi.org/10.3390/d15030320

Gentili R, Ferrè C, Cardarelli E, Montagnani C, Bogliani G, Citterio S, Comolli R (2019) Comparing Negative Impacts of *Prunus serotina*, *Quercus rubra* and *Robinia pseudoacacia* on Native Forest Ecosystems. Forests 10: e842. https://doi.org/10.3390/f10100842

Godefroid S, Phartyal SS, Weyembergh G, Koedam N (2005) Ecological factors controlling the abundance of non-native invasive black cherry (*Prunus serotina*) in deciduous forest understory in Belgium. Forest Ecology and Management 210: 91–105. https://doi.org/10.1016/j.foreco.2005.02.024

Halarewicz A (2011) The reasons underlying the invasion of forest communities by black cherry, *Prunus serotina* and its subsequent consequences. Forest Research Papers 72: 267–272. https://doi.org/10.2478/v10111-011-0026-5

Halarewicz A (2012) Właściwości Ekologiczne i Skutki Rozprzestrzeniania się Czeremchy Amerykańskiej *Padus serotina* (Ehrh.) Borkh. w wybranych fitocenozach leśnych. Wydawnictwo Uniwersytetu Przyrodniczego, Wrocław, 143 pp.

Halarewicz A, Pruchniewicz D (2015) Vegetation and environmental changes in a Scots pine forest invaded by *Prunus serotina*: What is the threat to terricolous bryophytes? European Journal of Forest Research 134: 793–801. https://doi.org/10.1007/s10342-015-0890-2

Halarewicz A, Żołnierz L (2014) Changes in the understorey of mixed coniferous forest plant communities dominated by the American black cherry (*Prunus serotina* Ehrh.). Forest Ecology and Management 313: 91–97. https://doi.org/10.1016/j.foreco.2013.11.006

Hao M, Zhang C, Zhao X, Von Gadow K (2018) Functional and phylogenetic diversity determine woody productivity in a temperate forest. Ecology and Evolution 8: 2395–2406. https://doi.org/10.1002/ece3.3857

Heberling JM, Cassidy ST, Fridley JD, Kalisz S (2019) Carbon gain phenologies of spring-flowering perennials in a deciduous forest indicate a novel niche for a widespread invader. The New Phytologist 221: 778–788. https://doi.org/10.1111/nph.15404

Heinrich G (1976) Flowering phenologies: Bog, woodland, anddisturbed habitats. Ecology 57: 890–899. https://doi.org/10.2307/1941055

Hejda M, Hanzelka J, Kadlec T, Štrobl M, Pyšek P, Reif J (2017) Impacts of an invasive tree across trophic levels: Species richness, community composition and resident species' traits. Diversity and Distributions 23: 997–1007. https://doi.org/10.1111/ddi.12596

Hermy M, Honnay O, Firbank L, Grashof-Bokdam C, Lawesson JE (1999) An ecological comparison between ancient and other forest plant species of Europe, and the implications for forest conservation. Biological Conservation 91: 9–22. https://doi.org/10.1016/S0006-3207(99)00045-2

Hisano M, Searle EB, Chen HYH (2018) Biodiversity as a solution to mitigate climate change impacts on the functioning of forest ecosystems. Biological Reviews of the Cambridge Philosophical Society 93: 439–456. https://doi.org/10.1111/brv.12351

Horodecki P, Nowiński M, Jagodziński AM (2019) Advantages of mixed tree stands in restoration of upper soil layers on postmining sites: A five-year leaf litter decomposition experiment. Land Degradation & Development 30: 3–13. https://doi.org/10.1002/ldr.3194

Jagodziński AM, Oleksyn J (2009) Ecological consequences of silviculture at variable stand densities. III. Stand stability, phytoclimate and biodiversity. Sylwan 153: 219–230.

Jagodziński AM, Dyderski MK, Gęsikiewicz K, Horodecki P (2018) Tree- and Stand-Level Biomass Estimation in a *Larix decidua* Mill. Chronosequence. Forests 9: e587. https://doi.org/10.3390/f9100587

Jagodziński AM, Dyderski MK, Gęsikiewicz K, Horodecki P (2019) Effects of stand features on aboveground biomass and biomass conversion and expansion factors based on a *Pinus sylvestris* L. chronosequence in Western Poland. European Journal of Forest Research 138: 673–683. https://doi.org/10.1007/s10342-019-01197-z

Jagodziński AM, Horodecki P, Jasińska AK, Maliński T, Pilarek Z, Woźniak K, Wrońska-Pilarek D, Zieliński J, Dyderski MK (2024) Invasive × *Sorbaronia fallax* nothosubsp. *mitschurinii* affects temperate Scots pine forest biodiversity and functioning. Forest Ecology and Management 568: e122147. https://doi.org/10.1016/j.foreco.2024.122147

Jiang P, Chen Y, Cao Y (2017) C:N:P Stoichiometry and Carbon Storage in a Naturally-Regenerated Secondary *Quercus variabilis* Forest Age Sequence in the Qinling Mountains, China. Forests 8: e281. https://doi.org/10.3390/f8080281

Jin Y, Qian H (2022) V.PhyloMaker2: An updated and enlarged R package that can generate very large phylogenies for vascular plants. Plant Diversity 44: 335–339. https://doi.org/10.1016/j.pld.2022.05.005

Kambel SW, Cowan PD, Helmus MR, Cornwell WK, Morlon H, Ackerly SP, Blomberg SP, Webb CO (2010) Picante: R tools for integrating phylogenies and ecology. Bioinformatics 26: 1463–1464. https://doi.org/10.1093/bioinformatics/btq166

Kato-Noguchi H, Kato M (2024) Invasive Characteristics of *Robinia pseudoacacia* and Its Impacts on Species Diversity. Diversity 16: e773. https://doi.org/10.3390/d16120773

Kleyer M, Bekker RM, Knevel IC, Bakker JP, Thompson K, Sonnenschein M, Poschlod P, van Groenendael JM, Klimeš L, Klimešová J, Klotz S, Rusch GM, Hermy M, Adriaens D, Boedeltje G, Bossuyt B, Dannemann A, Endels P, Götzenberger L, Hodgson JG, Jackel A-K, Kühn I, Kunzmann D, Ozinga WA, Römermann C, Stadler M, Schlegelmilch J, Steendam HJ, Tackenberg O, Wilmann B, Cornelissen JHC, Eriksson O, Garnier E, Peco B (2008) The LEDA Traitbase: A database of life-history traits of the Northwest European flora. Journal of Ecology 96: 1266–1274. https://doi.org/10.1111/j.1365-2745.2008.01430.x

Klotz S, Kühn I, Durka W (2002) BIOLFLOR – Eine Datenbank zu biologisch-ökologischen Merkmalen der Gefäßpflanzen in Deutschland. Schriftenreihe für Vegetationskunde. Bundesamt für Naturschutz, Bonn.

Kowarik I, Hiller A, Planchuelo G, Seitz B, Von Der Lippe M, Buchholz S (2019) Emerging Urban Forests: Opportunities for Promoting the Wild Side of the Urban Green Infrastructure. Sustainability 11: e6318. https://doi.org/10.3390/su11226318

Kudo G, Ida TY, Tani T (2008) Linkages between phenology, pollination, photosynthesis, and reproduction in deciduous forest understory plants. Ecology 89: 321–331. https://doi.org/10.1890/06-2131.1

Laliberté E, Legendre P (2010) A distance-based framework for measuring functional diversity from multiple traits. Ecology 91: 299–305. https://doi.org/10.1890/08-2244.1

Langmaier M, Lapin K (2020) A Systematic review of the impact of invasive alien plants on forest regeneration in european temperate forests. Frontiers in Plant Science 11: e524969. https://doi.org/10.3389/fpls.2020.524969

Lazzaro L, Mazza G, d'Errico G, Fabiani A, Giuliani C, Inghilesi AF, Lagomarsino A, Landi S, Lastrucci L, Pastorelli R, Roversi PF, Torrini G, Tricarico E, Foggi B (2018) How ecosystems change following invasion by *Robinia pseudoacacia*: Insights from soil chemical properties and soil microbial, nematode, microarthropod and plant communities. The Science of the Total Environment 622–623: 1509–1518. https://doi.org/10.1016/j.scitotenv.2017.10.017

Li Z, Mao C, Wu Q, Peng Y, Wang J, Zhang B, Zhang S, Liang X, Yan W, Chen X (2024) Temporal Variations in Aboveground Biomass, Nutrient Content, and Ecological Stoichiometry in Young and Middle-Aged Stands of Chinese Fir Forests. Plants 13: e1877. https://doi.org/10.3390/plants13131877

Li D, Belitz M, Campbell L, Guralnick R (2025) Extreme weather events have strong but different impacts on plant and insect phenology. Nature Climate Change. https://doi.org/10.1038/s41558-025-02248-7

López-Núñez FA, Heleno RH, Ribeiro S, Marchante H, Marchante E (2017) Four-trophic level food webs reveal the cascading impacts of an invasive plant targeted for biocontrol. Ecology 98(3): 782–793. https://doi.org/10.1002/ecy.1701

Lüdecke D (2018) ggeffects: Tidy data frames of marginal effects from regression models. Journal of Open Source Software 3: e772. https://doi.org/10.21105/joss.00772

Maitner BS, Boyle B, Casler N, Condit R, Donoghue J, Durán SM, Guaderrama D, Hinchliff CE, Jørgensen PM, Kraft NJB, McGill B, Merow C, Morueta-Holme N, Peet RK, Sandel B, Schild-

hauer M, Smith SA, Svenning J, Thiers B, Violle C, Wiser S, Enquist BJ (2018) The bien r package: A tool to access the Botanical Information and Ecology Network (BIEN) database. Methods in Ecology and Evolution 9: 373–379. https://doi.org/10.1111/2041-210X.12861

Martin GD (2019) Addressing geographical bias: A review of *Robinia pseudoacacia* (black locust) in the Southern Hemisphere. South African Journal of Botany 125: 481–492. https://doi.org/10.1016/j.sajb.2019.08.014

Matuszkiewicz W (2001) Przewodnik do oznaczania zbiorowisk roślinnych Polski. Wydawnictwo Naukowe PWN.

Miller JR, White HP, Chen JM, Peddle DR, McDermid G, Fournier RA, Shepherd P, Rubinstein I, Freemantle J, Soffer R, LeDrew E (1997) Seasonal change in understory reflectance of boreal forests and influence on canopy vegetation indices. Journal of Geophysical Research, D, Atmospheres 102: 29475–29482. https://doi.org/10.1029/97JD02558

Montecchiari S, Tesei G, Allegrezza M (2020) Effects of *Robinia pseudoacacia* coverage on diversity and environmental conditions of central-northern Italian *Quercus pubescens* sub-Mediterranean forests (habitat code 91AA*): a threshold assessment. Annali di Botanica: 33–54. https://doi.org/10.13133/2239-3129/16447

Mucina L, Bültmann H, Dierßen K, Theurillat J, Raus T, Čarni A, Šumberová K, Willner W, Dengler J, García RG, Chytrý M, Hájek M, Di Pietro R, Iakushenko D, Pallas J, Daniëls FJA, Bergmeier E, Santos Guerra A, Ermakov N, Valachovič M, Schaminée JHJ, Lysenko T, Didukh YP, Pignatti S, Rodwell JS, Capelo J, Weber HE, Solomeshch A, Dimopoulos P, Aguiar C, Hennekens SM, Tichý L (2016) Vegetation of Europe: hierarchical floristic classification system of vascular plant, bryophyte, lichen, and algal communities. Applied Vegetation Science 19: 3–264. https://doi.org/10.1111/avsc.12257

Namura-Ochalska A, Borowa B (2015) Walka z czeremchą amerykańską *Padus serotina* (Ehrh.) Borkh. w leśnictwie Rózin w Kampinoskim Parku Narodowym; ocena skuteczności wybranych metod. In: Krzysztofiak L, Krzysztofiak A (Eds) Inwazyjne Gatunki Obcego Pochodzenia Zagrożeniem dla rodzimej Przyrody red. Stowarzyszenie "Człowiek i Przyroda," Krzywe, 127–142.

Noh NJ, Son Y, Koo JW, Seo KW, Kim RH, Lee YY, Yoo KS (2010) Comparison of nitrogen fixation for North- and South-facing *Robinia pseudoacacia* stands in Central Korea. Journal of Plant Biology 53: 61–69. https://doi.org/10.13133/2239-3129/16447

Novoa A, Richardson DM, Pyšek P, Meyerson LA, Bacher S, Canavan S, Catford JA, Čuda J, Essl F, Foxcroft LC, Genovesi P, Hirsch H, Hui C, Jackson MC, Kueffer C, Le Roux JJ, Measey J, Mohanty NP, Moodley D, Müller-Schärer H, Packer JG, Pergl J, Robinson TB, Saul W-C, Shackleton RT, Visser V, Weyl OLF, Yannelli FA, Wilson JRU (2020) Invasion syndromes: A systematic approach for predicting biological invasions and facilitating effective management. Biological Invasions 22: 1801–1820. https://doi.org/10.1007/s10530-020-02220-w

Nyssen B, Vanhellemont M (2016) 5.6 Integrating black cherry in forest management in the Netherlands and Belgium. In: Krumm F, Vítková L (Eds) Introduced Tree Species in European Forests: Opportunities and Challenges. European Forest Institute, 362–372.

Nyssen B, Ouden JD, Bindewald A, Brancalion P, Kremer K, Lapin K, Raats L, Schatzdorfer E, Stanturf J, Verheyen K, Muys B (2024) Established Invasive Tree Species Offer Opportunities for Forest Resilience to Climate Change. Current Forestry Reports 10: 456–486. https://doi.org/10.1007/s40725-024-00232-6

Oksanen J, Blanchet F, Kindt R (2018) vegan 2.3.3. – Community Ecology Package. http://CRAN.R-project.org/package=vegan

Parker IM, Simberloff D, Lonsdale WM, Goodell K, Wonham M, Kareiva PM, Williamson MH, Von Holle B, Moyle PB, Byers JE, Goldwasser L (1999) Impact: Toward a framework for understanding the ecological effects of invaders. Biological Invasions 1: 3–19. https://doi.org/10.1023/A:1010034312781

Perring MP, Diekmann M, Midolo G, Schellenberger Costa D, Bernhardt-Römermann M, Otto JCJ, Gilliam FS, Hedwall P-O, Nordin A, Dirnböck T, Simkin SM, Máliš F, Blondeel H, Brunet J, Chudomelová M, Durak T, De Frenne P, Hédl R, Kopecký M, Landuyt D, Li D, Manning P, Petřík P, Reczyńska K, Schmidt W, Standovár T, Świerkosz K, Vild O, Waller DM, Verheyen K (2018) Understanding context dependency in the response of forest understorey plant communities to nitrogen deposition. Environmental Pollution 242: 1787–1799. https://doi.org/10.1016/j.envpol.2018.07.089

Piwczyński M, Puchałka R, Ulrich W (2016) Influence of tree plantations on the phylogenetic structure of understorey plant communities. Forest Ecology and Management 376: 231–237. https://doi.org/10.1016/j.foreco.2016.06.011

Qiu L, Zhang X, Cheng J, Yin X (2010) Effects of black locust (*Robinia pseudoacacia*) on soil properties in the loessial gully region of the Loess Plateau, China. Plant and Soil 332: 207–217. https://doi.org/10.1007/s11104-010-0286-5

Rahmonov O (2009) The Chemical Composition of Plant Litter of Black Locust (*Robinia pseudoacacia* L.) and Its Ecological Role in Sandy Ecosystems. Shengtai Xuebao. Acta Ecologica Sinica 29: 237–243. https://doi.org/10.1016/j.chnaes.2009.08.006

Ratyńska H, Wojterska M, Brzeg A, Kołacz M (2010) Multimedialna Encyklopedia Zbiorowisk Roślinnych Polski.

Rautiainen M, Mõttus M, Heiskanen J, Akujärvi A, Majasalmi T, Stenberg P (2011) Seasonal reflectance dynamics of common understory types in a northern European boreal forest. Remote Sensing of Environment 115: 3020–3028. https://doi.org/10.1016/j.rse.2011.06.005

Rawlik K, Rawlik M, Jagodziński AM (2023) Seasonal dynamics of herbaceous layer biomass and its contribution to annual net primary production in an oak–hornbeam forest. Forest Ecology and Management 544: e121195. https://doi.org/10.1016/j.foreco.2023.121195

Rice SK, Westerman B, Federici R (2004) Impacts of the Exotic, Nitrogen-Fixing Black Locust (*Robinia pseudoacacia*) on Nitrogen- Cycling in a Pine-Oak Ecosystem. Plant Ecology 174: 97–107. https://doi.org/10.1023/B:VEGE.0000046049.21900.5a

Richardson DM, Pysek P, Rejmanek M, Barbour MG, Panetta FD, West CJ (2000) Naturalization and invasion of alien plants: Concepts and definitions. Diversity & Distributions 6: 93–107. https://doi.org/10.1046/j.1472-4642.2000.00083.x

Ritchie JC (1956) *Vaccinium myrtillus* L. Journal of Ecology 44: e291. https://doi.org/10.2307/2257181

Roy HE, Pauchard A, Stoett PJ, Renard Truong T, Meyerson LA, Bacher S, Galil BS, Hulme PE, Ikeda T, Kavileveettil S, McGeoch MA, Nuñez MA, Ordonez A, Rahlao SJ, Schwindt E, Seebens H, Sheppard AW, Vandvik V, Aleksanyan A, Ansong M, August T, Blanchard R, Brugnoli E, Bukombe JK, Bwalya B, Byun C, Camacho-Cervantes M, Cassey P, Castillo ML, Courchamp F, Dehnen-Schmutz K, Zenni RD, Egawa C, Essl F, Fayvush G, Fernandez RD, Fernandez M, Foxcroft LC, Genovesi P, Groom QJ, González AI, Helm A, Herrera I, Hiremath AJ, Howard PL, Hui C, Ikegami M, Keskin E, Koyama A, Ksenofontov S, Lenzner B, Lipinskaya T, Lockwood JL, Mangwa DC, Martinou AF, McDermott SM, Morales CL, Müllerová J, Mungi NA, Munishi LK, Ojaveer H, Pagad SN, Pallewatta NPKTS, Peacock LR, Per E, Pergl J, Preda C, Pyšek P, Rai RK, Ricciardi A, Richardson DM, Riley S, Rono BJ, Ryan-Colton E, Saeedi H, Shrestha BB, Simberloff D, Tawake A, Tricarico E, Vanderhoeven S, Vicente J, Vilà M, Wanzala W, Werenkraut V, Weyl OLF, Wilson JRU, Xavier RO, Ziller SR (2024) Curbing the major and growing threats from invasive alien species is urgent and achievable. Nature Ecology & Evolution 8: 1216–1223. https://doi.org/10.1038/s41559-024-02412-w

Sádlo J, Vítková M, Pergl J, Pyšek P (2017) Towards site-specific management of invasive alien trees based on the assessment of their impacts: The case of *Robinia pseudoacacia*. NeoBiota 35: 1–34. https://doi.org/10.3897/neobiota.35.11909

Sapsford SJ, Brandt AJ, Davis KT, Peralta G, Dickie IA, Gibson RD, Green JL, Hulme PE, Nuñez MA, Orwin KH, Pauchard A, Wardle DA, Peltzer DA (2020) Towards a framework for under-

standing the context dependence of impacts of non-native tree species. Functional Ecology 34: 944–955. https://doi.org/10.1111/1365-2435.13544

Schooler SS, McEvoy PB, Coombs EM (2006) Negative per capita effects of purple loosestrife and reed canary grass on plant diversity of wetland communities. Diversity & Distributions 12: 351–363. https://doi.org/10.1111/j.1366-9516.2006.00227.x

Šibíková M, Jarolímek I, Hegedüšová K, Májeková J, Mikulová K, Slabejová D, Škodová I, Zaliberová M, Medvecká J (2019) Effect of planting alien *Robinia pseudoacacia* trees on homogenization of Central European forest vegetation. The Science of the Total Environment 687: 1164–1175. https://doi.org/10.1016/j.scitotenv.2019.06.043

Sitzia T, Campagnaro T, Kotze DJ, Nardi S, Ertani A (2018) The invasion of abandoned fields by a major alien tree filters understory plant traits in novel forest ecosystems. Scientific Reports 8: e8410. https://doi.org/10.1038/s41598-018-26493-3

Slabejová D, Bacigál T, Hegedüšová K, Májeková J, Medvecká J, Mikulová K, Šibíková M, Škodová I, Zaliberová M, Jarolímek I (2019) Comparison of the understory vegetation of native forests and adjacent *Robinia pseudoacacia* plantations in the Carpathian-Pannonian region. Forest Ecology and Management 439: 28–40. https://doi.org/10.1016/j.foreco.2019.02.039

Slabejová D, Čejka T, Hegedüšová K, Májeková J, Medvecká J, Mikulová K, Šibíková M, Škodová I, Šustek Z, Jarolímek I (2023) Comparison of alien *Robinia pseudoacacia* stands with native forest stands across different taxonomic groups. Forest Ecology and Management 548: e121413. https://doi.org/10.1016/j.foreco.2023.121413

Starfinger U, Kowarik I, Rode M, Schepker H (2003) From desirable ornamental plant to pest to accepted addition to the flora? – The perception of an alien tree species through the centuries. Biological Invasions 5: 323–335. https://doi.org/10.1023/B:BINV.0000005573.14800.07

Stekhoven DJ, Buhlmann P (2012) MissForest–non-parametric missing value imputation for mixed-type data. Bioinformatics 28: 112–118. https://doi.org/10.1093/bioinformatics/btr597

Stephenson AG (1981) Flower and fruit abortion: Proximate causes and ultimate functions. Annual Review of Ecology and Systematics 12: 253–279. https://doi.org/10.1146/annurev.es.12.110181.001345

Swenson NG, Enquist BJ (2009) Opposing assembly mechanisms in a Neotropical dry forest: Implications for phylogenetic and functional community ecology. Ecology 90: 2161–2170. https://doi.org/10.1890/08-1025.1

Tonkin JD, Bogan MT, Bonada N, Rios-Touma B, Lytle DA (2017) Seasonality and predictability shape temporal species diversity. Ecology 98: 1201–1216. https://doi.org/10.1002/ecy.1761

Trentanovi G, Ziechmann U, Kowarik I, Cierjacks A (2013) Biotic homogenization at the community scale: Disentangling the roles of urbanization and plant invasion. Diversity & Distributions 19(7): 738–748. https://doi.org/10.1111/ddi.12028

Tucker CM, Cadotte MW, Carvalho SB, Davies TJ, Ferrier S, Fritz SA, Grenyer R, Helmus MR, Jin LS, Mooers AO, Pavoine S, Purschke O, Redding DW, Rosauer DF, Winter M, Mazel F (2017) A guide to phylogenetic metrics for conservation, community ecology and macroecology: A guide to phylogenetic metrics for ecology. Biological Reviews of the Cambridge Philosophical Society 92: 698–715. https://doi.org/10.1111/brv.12252

Verheyen K, Vanhellemont M, Stock T, Hermy M (2007) Predicting patterns of invasion by black cherry (*Prunus serotina* Ehrh.) in Flanders (Belgium) and its impact on the forest understorey community. Diversity & Distributions 13: 487–497. https://doi.org/10.1111/j.1472-4642.2007.00334.x

Vilà M, Trillo A, Castro-Díez P, Gallardo B, Bacher S (2024) Field studies of the ecological impacts of invasive plants in Europe. NeoBiota 90: 139–159. https://doi.org/10.3897/neobiota.90.112368

Violle C, Navias M-L, Vile D, Kazakou E, Fortunel C, Hummel I, Garnier E (2007) Let the concept of trait be functional! Oikos 116: 882–892. https://doi.org/10.1111/j.0030-1299.2007.15559.x

Vítková M, Müllerová J, Sádlo J, Pergl J, Pyšek P (2017) Black locust (*Robinia pseudoacacia*) beloved and despised: A story of an invasive tree in Central Europe. Forest Ecology and Management 384: 287–302. https://doi.org/10.1016/j.foreco.2016.10.057

Von Holle B, Neill C, Largay EF, Budreski KA, Ozimec B, Clark SA, Lee K (2013) Ecosystem legacy of the introduced N_2-fixing tree *Robinia pseudoacacia* in a coastal forest. Oecologia 172: 915–924. https://doi.org/10.1007/s00442-012-2543-1

Wagner V, Chytrý M, Jiménez-Alfaro B, Pergl J, Hennekens S, Biurrun I, Knollová I, Berg C, Vassilev K, Rodwell JS, Škvorc Ž, Jandt U, Ewald J, Jansen F, Tsiripidis I, Botta-Dukát Z, Casella L, Attorre F, Rašomavičius V, Ćušterevska R, Schaminée JHJ, Brunet J, Lenoir J, Svenning J, Kącki Z, Petrášová-Šibíková M, Šilc U, García-Mijangos I, Campos JA, Fernández-González F, Wohlgemuth T, Onyshchenko V, Pyšek P (2017) Alien plant invasions in European woodlands. Diversity and Distributions 23: 969–981. https://doi.org/10.1111/ddi.12592

Webb CO, Peart DR (2000) Habitat associations of trees and seedlings in a Bornean rain forest. Journal of Ecology 88: 464–478. https://doi.org/10.1046/j.1365-2745.2000.00462.x

Webb CO, Ackerly DD, McPeek MA, Donoghue MJ (2002) Phylogenies and Community Ecology. Annual Review of Ecology and Systematics 33: 475–505. https://doi.org/10.1146/annurev.ecolsys.33.010802.150448

Wild J, Kaplan Z, Danihelka J, Petřík P, Chytrý M, Novotný P, Rohn M, Šulc V, Brůna J, Chobot K, Ekrt L, Holubová D, Knollová I, Kocián P, Štech M, Štěpánek J, Zouhar V (2019) Plant distribution data for the Czech Republic integrated in the Pladias database. Preslia 91: 1–24. https://doi.org/10.23855/preslia.2019.001

Wohlgemuth T, Gossner MM, Campagnaro T, Marchante H, van Loo M, Vacchiano G, Castro-Díez P, Dobrowolska D, Gazda A, Keren S, Keserű Z, Koprowski M, La Porta N, Marozas V, Nygaard PH, Podrázský V, Puchałka R, Reisman-Berman O, Straigytė L, Ylioja T, Pötzelsberger E, Silva JS (2022) Impact of non-native tree species in Europe on soil properties and biodiversity: A review. NeoBiota 78: 45–69. https://doi.org/10.3897/neobiota.78.87022

Woziwoda B, Kopeć D, Witkowski J (2014) The negative impact of intentionally introduced *Quercus rubra* L. on a forest community. Acta Societatis Botanicorum Poloniae 83: 39–49. https://doi.org/10.5586/asbp.2013.035

Woziwoda B, Dyderski MK, Jagodziński AM (2019) Effects of land use change and *Quercus rubra* introduction on *Vaccinium myrtillus* performance in *Pinus sylvestris* forests. Forest Ecology and Management 440: 1–11. https://doi.org/10.1016/j.foreco.2019.03.010

Woziwoda B, Dyderski MK, Jagodziński AM (2021) Forest land use discontinuity and northern red oak *Quercus rubra* introduction change biomass allocation and life strategy of lingonberry *Vaccinium vitis-idaea*. Forest Ecosystems 8: 1–9. https://doi.org/10.1186/s40663-021-00287-y

Yan P, Lu X, Li W, Zhang J, Li P, Li Y, Wang K, Ding S (2023) Seasonal Variations in Plant Species Diversity and Phylogenetic Diversity in Abandoned Farmland of China's Huang–Huai Plain. Diversity 15: e922. https://doi.org/10.3390/d15080922

Zasada M (2017) Raport końcowy z tematu badawczego "Ekologiczne, gospodarcze i urządzeniowe konsekwencje występowania wybranych gatunków drzew obcych w Polsce" realizowanego w latach 2013-2017 przez Samodzielną Pracownię Dendrometrii i Nauki o Produkcyjności Lasu na zlecenie Dyrekcji Generalnej Lasów Państwowych w Warszawie. SGGW, Warszawa.

Supplementary material 1

Supplementary information

Authors: Sebastian Bury, Marcin K. Dyderski

Data type: docx

Explanation note: **table S1.** The mean diameter in breast height (DBH) for trees with DBH<5cm, calculated. **table S2.** List of all woody species present in study plots and allometric models used for foliage biomass estimation (table S3). **table S3.** Allometric equations determining the biomass of particular tree species recorded on the study plots. **figure S1.** Distribution of the study plots (n = 160). **table S4.** General characteristics of the studied plots: stand age, total aboveground biomass, invasive tree species aboveground biomass. **figure S2.** Histogram showing the distribution of invasive species aboveground biomass [Mg ha-1] in plots with *P. serotina* (n = 64), and plots with *R. pseudoacacia* (n= 64). **table S5.** Functional traits used in the study and their min/max/mean values, standard error (SE), coefficient of variation (CV) and completness for numeric traits, and number of classes, frequency and completness for categorical traits. **table S6.** Results of Threshold Indicator Taxa Analysis for *R. pseudoacacia* in nutrient-poor sites in spring. **table S7.** Results of Threshold Indicator Taxa Analysis for *R. pseudoacacia* in nutrient-rich in spring. **table S8.** Results of Threshold Indicator Taxa Analysis for *P. serotina* in nutrient-poor sites in spring. **table S9.** Results of Threshold Indicator Taxa Analysis for *P. serotina* in nutrient-rich sites in spring. **table S10.** Results of Threshold Indicator Taxa Analysis for *R. pseudoacacia* in nutrient-poor sites in summer. **table S11.** Results of Threshold Indicator Taxa Analysis for *R. pseudoacacia* in nutrient-rich sites in summer. **table S12.** Results of Threshold Indicator Taxa Analysis for *P. serotina* in nutrient-poor sites in summer. **table S13.** Results of Threshold Indicator Taxa Analysis for *P. serotina* in nutrient-rich sites in summer. **table S14.** The parameters of Generalized Linear Mixed-Effect Models for the impact of *R. pseudoacacia* aboveground biomass (AB) on different plant diversity indicators on nutrient-poor sites in spring. **table S15.** The parameters of Generalized Linear Mixed-Effect Models for the impact of *R. pseudoacacia* aboveground biomass (AB) on different plant diversity indicators on nutrient-rich sites in spring. **table S16.** The parameters of Generalized Linear Mixed-Effect Models for the impact of *P. serotina* aboveground biomass (AB) on different plant diversity indicators on nutrient-poor sites in spring. **table S17.** The parameters of Generalized Linear Mixed-Effect Models for the impact of *P. serotina* aboveground biomass (AB) on different plant diversity indicators on nutrient-rich sites in spring. **table S18.** The parameters of Generalized Linear Mixed-Effect Models for the impact of *R. pseudoacacia* aboveground biomass (AB) on different plant diversity indicators on nutrient-poor sites in summer. **table S19.** The parameters of Generalized Linear Mixed-Effect Models for the impact of *R. pseudoacacia* aboveground biomass (AB) on different plant diversity indicators on nutrient-rich sites in summer. **table S20.** The parameters of Generalized Linear Mixed-Effect Models for the impact of *P. serotina* aboveground biomass (AB) on different plant diversity indicators on nutrient-poor sites in summer. **table S21.** The parameters of Generalized Linear Mixed-Effect Models for the impact of *P. serotina* aboveground biomass (AB) on different plant diversity indicators on nutrient-rich sites in summer.

Link: https://doi.org/10.3897/neobiota.100.151606.suppl1

Table S1. The mean diameter in breast height (DBH) for trees with DBH<5cm, calculated from 102 plots, n = number of measured trees. Reproduced from Bury and Dyderski (2025)

Species	Mean	n	SD	Remarks
Acer campestre L.	2.11	82	1.39	
Acer negundo L.	1.94	24	1.32	
Acer pseudoplatanus L.	1.43	261	1.32	Applied also for *A. platanoides*
Amelanchier spicata K.Koch	0.95	11	0.47	
×*Sorbaronia fallax* nothosubsp. *mitschurinii (*A.K.Skvortsov & Maitul.) Stalažs	1.08	5	0.72	
Betula pendula Roth	1.54	314	1.38	
Betula pubescens Ehrh.	0.20	1	0.00	
Carpinus betulus L.	1.88	246	1.49	
Carya ovata (Mill.) K.Koch	2.40	1	0.00	
Cerasus avium L.	2.41	6	1.28	
Cornus sanguinea L.	1.42	6	1.10	
Corylus avellana L.	1.60	421	1.13	
Crataegus laevigata DC.	1.68	28	1.19	
Crataegus monogyna Jacq.	1.59	56	0.96	
Crataegus rhipidophylla Gand.	1.45	14	0.81	
Euonymus europaeus L.	0.94	11	0.99	
Fagus sylvatica L.	1.71	259	1.30	
Frangula alnus Mill.	0.76	556	0.67	
Fraxinus excelsior L.	1.99	6	1.91	Applied also for *Syringa vulgaris*
Larix decidua Mill.	0.70	1	0.00	
Lonicera periclymenum L.	0.30	6	0.15	Applied also for *L. xylosteum*
Picea abies (L.) H.Karst.	2.27	8	1.02	
Pinus sylvestris L.	2.97	57	1.32	
Populus tremula L.	4.75	1	0.00	
Prunus cerasifera Ehrh.	0.51	9	0.53	
Prunus domestica L.	1.02	18	0.10	Applied also for *P. persica* and *P. spinosa*
Prunus mahaleb L.	2.00	1	0.00	
Prunus padus L.	1.06	1205	0.88	
Prunus serotina Ehrh.	1.31	3696	1.18	
Pseudotsuga menziesii Mirb.	4.02	3	0.88	
Pyrus pyraster (L.) Burgsd.	4.50	1	0.00	Applied also for *Malus* spp.
Quercus petraea (Matt.) Liebl.	1.58	342	1.25	
Quercus robur L.	2.58	79	1.26	
Quercus rubra L.	3.60	1	0.00	
Rhamnus cathartica L.	3.35	2	0.92	
Ribes spicatum Robson	0.30	1	0.00	
Ribes uva-crispa L.	0.29	9	0.03	Applied also for *R. rubrum* and *Rosa canina*
Robinia pseudoacacia L.	1.83	1036	1.38	
Sambucus nigra L.	1.80	98	1.22	
Sambucus racemosa L.	0.98	4	0.31	
Sorbus aucuparia L.	1.74	880	1.29	
Tilia cordata Mill.	1.45	102	1.22	
Tilia platyphyllos Scop.	2.20	3	2.23	
Ulmus minor Mill.	1.96	47	1.20	Applied also for other *Ulmus* spp.

Table S2. List of all woody species present in study plots and allometric models used for foliage biomass estimation (**Table S3**). Reproduced from Bury and Dyderski (2025)

Species	**Taxa group**
×*Sorbaronia fallax* nothosubsp. *mitschurinii (*A.K.Skvortsov & Maitul.) Stalažs	*Cornus*
Acer campestre L.	*Acer*
Acer negundo L.	*Acer*
Acer platanoides L.	*Acer*
Acer pseudoplatanus L.	*Acer*
Aesculus hippocastanum L.	Broadleaved
Alnus glutinosa L.	*Alnus*
Amelanchier spicata K.Koch	*Amelanchier*
Betula pendula Roth	*Betula*
Betula pubescens Ehrh.	*Betula*
Carpinus betulus L.	*Carpinus*
Carya ovata (Mill.) K.Koch	Broadleaved
Cerasus avium L.	*Prunus serotina, Prunus*
Cornus sanguinea L.	*Cornus sanguinea*
Corylus avellana L.	*Corylus avellana*
Crataegus laevigata DC.	*Prunus serotina*
Crataegus monogyna Jacq.	*Prunus serotina, Prunus*
Crataegus rhipidophylla Gand.	*Prunus serotina, Prunus*
Euonymus europaeus L.	*Cornus sanguinea*
Fagus sylvatica L.	*Fagus*
Frangula alnus Mill.	*Frangula alnus*
Fraxinus excelsior L.	*Fraxinus*
Larix decidua Mill.	*Larix*
Lonicera periclymenum L.	*Cornus sanguinea*
Lonicera xylosteum L.	*Cornus sanguinea*
Malus domestica Borkh.	*Prunus serotina*
Malus sylvestris (L.) Mill.	*Prunus serotina*
Picea abies (L.) H.Karst.	*Picea*
Pinus sylvestris L.	*Pinus*
Populus tremula L.	*Populus*
Prunus cerasifera Ehrh.	*Prunus serotina*
Prunus domestica L.	*Prunus serotina*
Prunus mahaleb L.	*Prunus serotina*
Prunus padus L.	*Prunus serotina, Prunus*
Prunus persica (L.) Batsch	*Prunus serotina*
Prunus serotina Ehrh.	*Prunus serotina, Prunus*
Prunus spinosa L.	*Prunus serotina*
Pseudotsuga menziesii Mirb.	*Picea*
Pyrus pyraster (L.) Burgsd.	*Prunus serotina*
Quercus cerris L.	*Quercus*
Quercus petraea (Matt.) Liebl.	*Quercus*
Quercus robur L.	*Quercus*
Quercus rubra L.	*Quercus*
Rhamnus cathartica L.	*Cornus sanguinea*
Ribes rubrum L.	*Ribes*
Ribes spicatum Robson	*Ribes*
Ribes uva-crispa L.	*Ribes*

Robinia pseudoacacia L.	*Robinia*
Rosa canina L.	*Cornus sanguinea*
Salix alba L.	Broadleaved
Sambucus nigra L.	*Sambucus nigra*
Sambucus racemosa L.	*Sambucus nigra*
Sorbus aucuparia L.	*Sorbus aucuparia*
Syringa vulgaris L.	*Cornus sanguinea*
Tilia cordata Mill.	Broadleaved
Tilia platyphyllos Scop.	Broadleaved
Ulmus glabra Huds.	*Ulmus*
Ulmus laevis Pall.	*Ulmus*
Ulmus minor Mill.	*Ulmus*

Table S3. Allometric equations determining the biomass of particular tree species recorded on the study plots. Equations adopted were established for habitat conditions similar to those of this study. Abbreviations: DBH – diameter at breast height; CF - correction factor to reverse transformation of log-log models. Biomass components: AB – total aboveground biomass (ABW+FL), ABW – aboveground woody biomass, FL – foliage biomass. Taxa group is referenced to particular species in **Table S2**. Reproduced from Bury and Dyderski (2025)

Taxa group	Biomass component	Unit	Source	R^2	N	DBH min [cm]	DBH max [cm]	Formula	a	b	CF
Acer	ABW	kg	Forrester et al. 2017	0.941	231	0	25	ln(Y)=ln(a)+b*ln(D), CF	-2.31160	2.41860	1.01050
Acer	ABW	kg	Forrester et al. 2017	0.969	3521	25	88	ln(Y)=ln(a)+b*ln(D), CF	-2.16530	2.41430	1.04148
Acer	FL	kg	Forrester et al. 2017	0.789	70	0	88	ln(Y)=ln(a)+b*ln(D), CF	-4.06250	2.06620	1.00318
Alnus	ABW	kg	Forrester et al. 2017	0.982	231	0	28.3	ln(Y)=ln(a)+b*ln(D), CF	-2.29180	2.40280	0.97779
Alnus	FL	kg	Forrester et al. 2017	0.578	231	0	28.3	ln(Y)=ln(a)+b*ln(D), CF	-4.46950	1.76230	0.97465
Amelanchier	AB	g	Brown 1976	0.990	39	0.4	4.5	ln(y)=a+b*ln(X)	3.60700	2.88700	NA
Amelanchier	FL	g	Brown 1976	0.830	39	0.4	4.5	ln(y)=a+b*ln(X)	1.69100	2.11100	NA
Betula	ABW	kg	Forrester et al. 2017	0.988	449	0	38	ln(Y)=ln(a)+b*ln(D), CF	-2.21180	2.37710	1.00799
Betula	FL	kg	Forrester et al. 2017	0.903	231	0	38	ln(Y)=ln(a)+b*ln(D), CF	-4.13700	1.88610	1.16321
Broadleaved	ABW	kg	Forrester et al. 2017	0.969	3521	0	88	ln(Y)=ln(a)+b*ln(D), CF	-2.16530	2.41430	1.04148
Broadleaved	FL	kg	Forrester et al. 2017	0.847	1824	0	88	ln(Y)=ln(a)+b*ln(D), CF	-4.22860	1.86250	1.06365
Carpinus betulus	AB	kg	Jagodziński, unpbl.	0.965	38	0	20	Y=a*D^b	0.04670	2.67655	NA
Carpinus betulus	FL	kg	Jagodziński, unpbl.	0.875	38	0	20	Y=a*D^b	0.01996	1.95261	NA
Cornus sanguinea	AB	kg	Jagodziński, unpbl.	0.892	52	0	8	Y=a*D^b	1.29073	1.23701	NA
Cornus sanguinea	FL	kg	Jagodziński, unpbl.	0.734	52	0	8	Y=a*D^b	0.13820	1.12562	NA
Corylus avellana	AB	kg	Jagodziński, unpbl.	0.926	96	0	16	Y=a*D^b	0.65347	1.37869	NA
Corylus avellana	FL	kg	Jagodziński, unpbl.	0.668	96	0	16	Y=a*D^b	0.09715	0.92685	NA
Fagus	ABW	kg	Forrester et al. 2017	0.975	712	0	82	ln(Y)=ln(a)+b*ln(D), CF	-1.78430	2.38950	1.09215
Fagus	FL	kg	Forrester et al. 2017	0.883	330	0	73	ln(Y)=ln(a)+b*ln(D), CF	-4.48130	1.90730	1.08752
Frangula alnus	AB	kg	Jagodziński, unpbl.	0.852	74	0	87	Y=a*D^b	0.16494	1.72121	NA
Frangula alnus	FL	kg	Jagodziński, unpbl.	0.704	74	0	87	Y=a*D^b	0.03785	0.94933	NA
Fraxinus	ABW	kg	Forrester et al. 2017	0.946	330	0	40	ln(Y)=ln(a)+b*ln(D), CF	-2.54360	2.61840	0.94631
Fraxinus	FL	kg	Forrester et al. 2017	0.872	158	0	69	ln(Y)=ln(a)+b*ln(D), CF	-4.85020	2.40640	0.80923
Larix	AB	kg	Jagodziński et al. 2018	0.971	96	2	58	Y=a*D^b	0.13800	2.39070	NA
Larix	FL	kg	Jagodziński et al. 2018	0.767	96	2	58	Y=a*D^b	0.00460	2.10360	NA
Picea	ABW	kg	Forrester et al. 2017	0.970	668	0	77	ln(Y)=ln(a)+b*ln(D), CF	-2.04640	2.30480	1.03300
Picea	FL	kg	Forrester et al. 2017	0.906	1007	0	77	ln(Y)=ln(a)+b*ln(D), CF	-2.79570	1.86880	1.02003

Pinus	AB	kg	Jagodziński et al. 2019	0.976	549	0	65	Y=a*D^b	0.20760	2.21850	NA
Pinus	FL	kg	Jagodziński et al. 2019	0.841	549	0	65	Y=a*D^b	0.03020	1.74200	NA
Populus	ABW	kg	Forrester et al. 2017	0.991	218	0	45	ln(Y)=ln(a)+b*ln(D), CF	-2.25670	2.36070	1.04492
Populus	FL	kg	Forrester et al. 2017	0.910	165	0	45	ln(Y)=ln(a)+b*ln(D), CF	-4.14540	1.94800	1.01172
Prunus	ABW	kg	Forrester et al. 2017	0.987	99	0	50	ln(Y)=ln(a)+b*ln(D), CF	-1.09680	2.09200	1.02629
Prunus	FL	kg	Forrester et al. 2017	0.545	99	0	50	ln(Y)=ln(a)+b*ln(D), CF	-4.10580	1.32120	0.95641
Prunus serotina	AB	kg	Jagodziński, unpbl.	0.974	50	0	15	Y=a*D^b	0.84778	1.44607	NA
Prunus serotina	FL	kg	Jagodziński, unpbl.	0.937	50	0	15	Y=a*D^b	0.04973	1.86895	NA
Quercus	ABW	kg	Forrester et al. 2017	0.990	579	0	77	ln(Y)=ln(a)+b*ln(D), CF	-2.31490	2.51330	1.03670
Quercus	FL	kg	Forrester et al. 2017	0.911	99	0	68	ln(Y)=ln(a)+b*ln(D), CF	-4.46630	2.13750	0.96633
Ribes	AB	g	Brown 1976	0.900	37	0.4	1.4	ln(y)=a+b*ln(X)	3.89200	3.12200	NA
Ribes	FL	g	Brown 1976	0.630	37	0.4	1.4	ln(y)=a+b*ln(X)	2.16400	2.53800	NA
Robinia	AB	kg	Zasada 2017	NA	22	7	46	Y=a*D^b	0.00030	2.51800	NA
Robinia	ABW	kg	Forrester et al. 2017	0.923	165	0	24	ln(Y)=ln(a)+b*ln(D), CF	-2.53440	2.45980	1.02110
Robinia	FL	kg	Forrester et al. 2017	0.936	99	0	24	ln(Y)=ln(a)+b*ln(D), CF	-2.79850	1.12780	1.02069
Robinia	FL	kg	Zasada 2017	NA	22	7	46	Y=a*D^b	0.00150	1.52880	NA
Sambucus nigra	AB	kg	Jagodziński, unpbl.	0.634	60	0	10	Y=a*D^b	1.34743	1.06650	NA
Sambucus nigra	FL	kg	Jagodziński, unpbl.	0.479	60	0	10	Y=a*D^b	0.18051	0.79876	NA
Sorbus aucuparia	AB	kg	Jagodziński, unpbl.	0.929	64	0	9	Y=a*D^b	0.15992	2.16383	NA
Sorbus aucuparia	FL	kg	Jagodziński, unpbl.	0.792	64	0	9	Y=a*D^b	0.02302	1.66533	NA
Ulmus	ABW	kg	Forrester et al. 2017	0.847	1824	0	88	ln(Y)=ln(a)+b*ln(D), CF	-4.22860	1.86250	1.06365
Ulmus	ABW	kg	Alberti et al. 2005	0.970	10	0	31	Y=a*D^b	0.10000	2.56000	NA
Ulmus	FL	kg	Forrester et al. 2017	0.969	3521	0	88	ln(Y)=ln(a)+b*ln(D), CF	-2.16530	2.41430	1.04148
Ulmus	FL	kg	Alberti et al. 2005	0.980	10	0	31	Y=a*D^b	0.13000	1.12000	NA

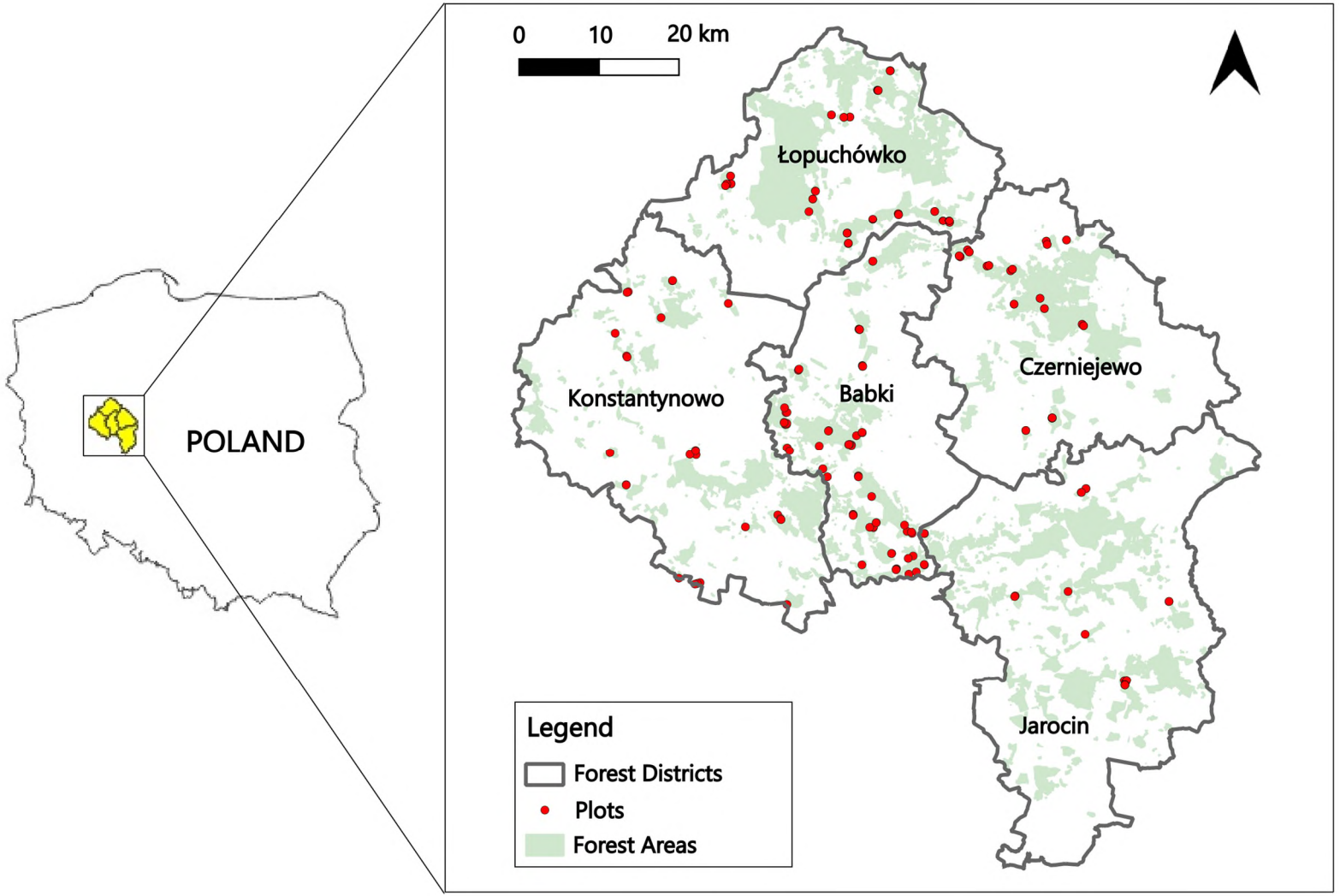

Figure S1. Distribution of the study plots (n = 160). The background map of forest cover comes from the Forest Data Bank (BDL 2024). Reproduced from Bury and Dyderski (2025)

Table S4. General characteristics of the studied plots: stand age, total aboveground biomass, invasive tree species aboveground biomass. *Quercus* ─ nutrient-rich habitats with *Q. petraea/robur*, *Pinus* ─ nutrient-poor habitats with *P. sylvestris.* Reproduced from Bury and Dyderski (2025)

	Stand age [years]				**Total Aboveground Biomass [Mg ha^{-1}]**				**Invader Aboveground Biomass [Mg ha^{-1}]**			
	Min.	Mean	SD	Max.	Min.	Mean	SD	Max.	Min.	Mean	SD	Max.
						Control						
Quercus	47	93.75	33.28	139	157.38	278.74	100.16	507.92	0.00	0.00	0.00	0.00
Pinus	50	76.00	22.82	117	142.95	187.17	34.50	254.63	0.00	0.00	0.00	0.00
						Prunus serotina						
Quercus	44	90.31	31.96	137	138.12	267.52	93.24	505.01	0.19	6.68	7.24	27.39
Pinus	45	71.59	21.78	108	142.37	196.99	33.25	256.66	0.18	7.34	8.75	47.11
						Robinia pseudoacacia						
Quercus	42	94.56	34.24	139	147.63	317.01	141.48	709.91	0.82	50.77	70.37	278.24
Pinus	42	76.81	23.06	117	125.32	182.14	31.44	246.52	0.22	20.91	31.69	153.00

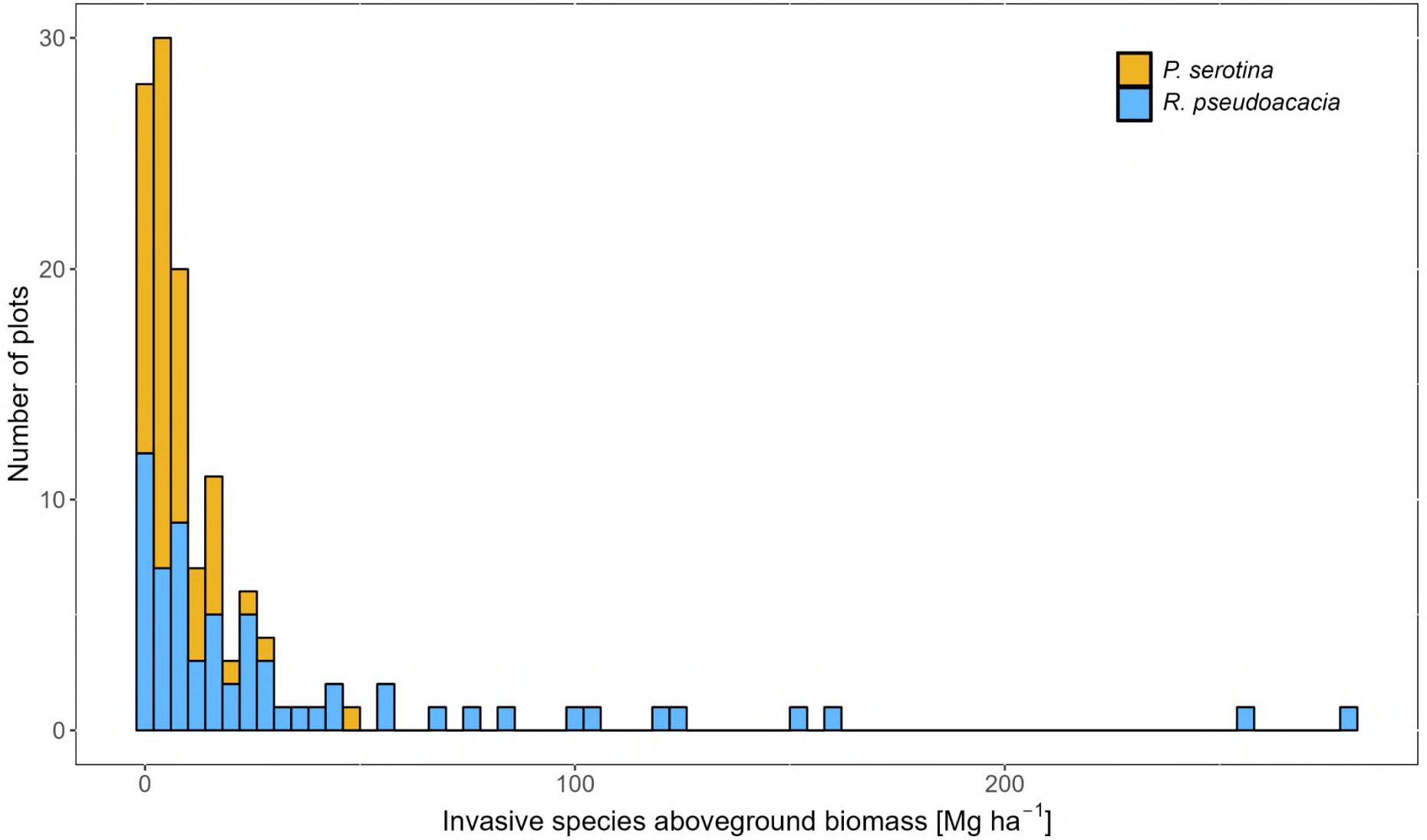
30
20
10
0
Number of plots
0
100
200
Invasive species aboveground biomass [Mg ha^{-1}]
P. serotina
R. pseudoacacia

Figure S2. Histogram showing the distribution of invasive species aboveground biomass [Mg ha^{-1}] in plots with *P. serotina* (n = 64), and plots with *R. pseudoacacia* (n= 64). In this graph we excluded control plots (n = 32) with no studied invasive species. Reproduced from Bury and Dyderski (2025)

Table S5. Functional traits used in the study and their min/max/mean values, standard error (SE), coefficient of variation (CV) and completness for numeric traits, and number of classes, frequency and completness for categorical traits

Numeric traits	**min**	**max**	**mean**	**SE**	**CV [%]**	**Completness [%]**
Light Ecological Indicator Value	1	9	5.59	0.11	28.6	97.6
Temperature Ecological Indicator Value	2	8	5.5	0.06	14.8	64.9
Moisture Ecological Indicator Value	2	10	5.22	0.08	22.8	82.0
Soil reaction Ecological Indicator Value	1	8	5.91	0.12	29.5	66.8
Soil fertility Ecological Indicator Value	1	9	5.36	0.13	35.9	84.4
Flowering beginning [months]	1	9	4.94	0.09	26.2	99.0
Flowering duration [months]	1	12	3.06	0.11	53.2	99.0
Specific leaf area (SLA) [cm^2 g^{-1}]	49.84	899.14	261.40	8.75	47.9	96.1
Seed mass (SM) [mg]	0.001	13737.621	232.657	93.718	576.7	96.1
Maximum height (H) [m]	0.03	91.44	7.98	1.04	187.3	99.0
Categorical traits	**Number of classes**	**Classes and their frequency**				**Completness [%]**
Life form	7	Hemicryptophyte = 43.9%; Phanerophyte = 29.8%; Therophyte = 9.8%; Geophyte = 8.8%; Chamaephyte = 3.9%; Liana = 3.4%; Hydrophyte = 0.5%				100,0
Pollination mode – insect	2	yes = 69.3%; no = 30.7%				97.1
Pollination mode – self-pollination	2	yes = 52.2%. no = 47.8%				97.1
Pollination mode – wind	2	yes = 32.7%. no = 67.3%				97.1

Table S6. Results of Threshold Indicator Taxa Analysis for *R. pseudoacacia* in nutrient-poor sites in spring

Species	ienv.cp	zenv.cp	freq	maxgrp	IndVal	zscore	5%	10%	50%	90%	95%	purity	reliability	z.median	filter
Acer platanoides	0.404	0.736	14	2	36.13	1.88	0.000	0.199	1.162	3.144	3.349	0.886	0.692	2.472	0
Acer pseudoplatanus	3.484	3.484	10	2	37.40	2.58	0.000	0.724	2.608	3.484	3.921	0.704	0.498	2.095	0
Alliaria petiolata	1.024	1.024	3	2	10.71	1.12	0.824	0.952	1.717	2.361	2.377	0.532	0.116	1.321	0
Anthoxanthum odoratum	1.717	1.336	10	2	32.40	3.16	1.172	1.336	1.717	3.412	3.484	0.960	0.826	3.412	0
Arrhenatherum elatius	3.484	3.484	3	2	19.31	1.87	0.000	0.000	2.377	3.484	3.484	0.842	0.408	2.327	0
Avenella flexuosa	2.288	2.288	24	1	41.94	0.88	0.000	0.000	1.717	3.349	3.616	0.592	0.442	1.801	0
Betula pendula	2.928	2.928	8	1	21.62	1.12	0.000	0.000	1.717	2.511	2.928	0.550	0.418	1.795	0
Brachypodium sylvaticum	0.000	0.000	5	2	14.71	0.79	0.000	0.000	1.063	2.471	3.156	0.594	0.298	1.621	0
Calamagrostis epigejos	0.000	0.000	24	1	56.19	1.56	0.000	0.000	2.559	3.685	3.880	0.250	0.594	2.198	0
Carpinus betulus	2.271	2.236	3	2	15.79	2.65	2.055	2.170	2.271	3.276	3.484	0.960	0.566	3.085	0
Chelidonium majus	2.742	2.742	14	1	29.78	0.58	0.000	0.000	1.055	2.768	3.484	0.636	0.350	1.497	0
Convallaria majalis	3.349	3.349	4	2	15.69	0.81	0.000	0.000	1.934	3.349	3.349	0.542	0.356	1.913	0
Dactylis glomerata	0.000	0.000	6	2	14.34	0.38	0.000	0.000	1.958	3.349	3.553	0.430	0.284	1.621	0
Dryopteris carthusiana	2.236	2.236	24	2	44.58	1.56	0.000	0.000	2.236	3.553	3.815	0.752	0.626	2.381	0
Dryopteris filix mas	1.717	1.717	3	2	13.04	1.92	1.106	1.280	1.717	2.236	2.271	0.808	0.306	2.034	0
Fagus sylvatica	3.225	3.225	5	2	34.45	3.78	1.819	1.981	3.092	3.304	3.616	0.990	0.838	4.592	0
Fallopia convolvulus	2.377	2.377	14	2	38.17	1.95	0.825	1.024	2.377	3.303	3.484	0.860	0.648	2.546	0
Festuca ovina	0.000	1.024	4	1	20.00	3.58	0.000	0.000	0.305	1.063	1.090	0.982	0.732	3.972	0
Festuca rubra	0.000	1.024	3	1	15.00	2.44	0.000	0.000	0.000	1.047	1.079	0.946	0.534	2.952	0
Frangula alnus	0.000	0.000	23	1	53.60	2.02	0.000	0.000	1.085	3.616	4.076	0.730	0.628	2.249	0
Fraxinus excelsior	3.484	0.000	4	2	11.76	0.58	0.000	0.000	1.162	3.547	3.616	0.668	0.298	1.887	0
Galeopsis tetrahit	0.000	0.000	10	1	31.91	1.18	0.000	0.000	1.008	3.105	3.480	0.516	0.394	1.711	0
Galium aparine	2.791	1.024	10	2	23.03	1.16	0.000	0.859	1.717	2.791	2.904	0.592	0.418	1.847	0
Geranium robertianum	0.000	0.000	18	2	44.13	2.71	0.000	0.531	1.162	2.693	2.928	0.920	0.836	3.034	0
Geum urbanum	1.024	1.024	4	2	14.29	1.64	0.736	0.935	1.162	2.271	2.287	0.570	0.356	2.013	0
Hedera helix	1.162	1.162	4	2	11.78	0.81	0.000	0.305	1.740	3.298	3.349	0.690	0.304	1.746	0
Holcus mollis	1.336	1.336	3	2	12.50	1.81	0.000	1.160	1.336	2.791	2.928	0.922	0.316	2.145	0
Humulus lupulus	2.059	2.059	6	1	17.68	1.46	0.000	0.089	1.958	3.231	3.685	0.490	0.396	1.982	0
Impatiens parviflora	0.000	1.024	14	2	32.63	1.98	0.000	0.089	1.151	2.791	2.905	0.814	0.764	2.920	0
Lactuca muralis	3.484	3.484	9	2	31.27	2.11	0.825	0.952	2.279	3.616	3.619	0.822	0.558	2.286	0
Maianthemum bifolium	0.000	0.000	3	1	16.22	2.25	0.000	0.000	0.000	2.271	2.271	0.830	0.434	2.473	0
Melampyrum pratense	3.349	0.935	11	1	23.19	0.77	0.000	0.603	2.115	3.172	3.225	0.540	0.502	1.990	0
Moehringia trinervia	1.162	1.162	25	2	53.29	2.27	0.000	0.736	1.162	2.791	3.411	0.882	0.798	2.961	0
Pilosella officinarum	2.791	2.791	3	2	15.20	2.38	0.000	0.000	2.766	3.412	3.685	0.692	0.466	2.868	0
Pinus sylvestris	0.000	0.000	12	1	39.77	1.41	0.000	0.000	2.203	3.092	3.156	0.804	0.544	2.202	0
Poa nemoralis	3.349	3.349	8	2	32.28	3.41	0.000	0.000	2.359	3.349	3.547	0.810	0.486	2.162	0
Prunus avium	2.559	2.559	6	2	14.92	0.77	0.000	0.000	2.469	3.616	4.076	0.634	0.384	2.113	0
Prunus domestica	0.935	0.935	3	1	15.79	2.57	0.000	0.000	0.935	1.008	1.047	0.956	0.544	3.301	0
Prunus padus	2.742	0.000	9	1	22.03	0.48	0.000	0.000	0.000	2.236	2.742	0.814	0.422	1.563	0
Prunus serotina	0.736	0.736	36	1	66.55	0.71	0.000	0.000	0.000	2.141	3.144	0.828	0.378	1.277	0

Pteridium aquilinum	0.000	0.000	3	1	12.96	1.63	0.000	0.000	0.000	2.470	2.559	0.774	0.434	2.310	0
Pyrus communis	2.288	2.288	4	1	12.90	1.01	0.000	0.000	1.717	2.361	2.380	0.640	0.210	1.633	0
Quercus petraea	3.349	3.349	34	1	70.35	1.62	0.000	1.040	2.815	3.361	3.480	0.642	0.564	1.971	0
Quercus robur	1.717	1.717	5	2	21.74	2.80	1.162	1.336	1.717	3.109	3.276	0.956	0.728	3.128	0
Ribes rubrum	3.484	3.349	3	2	14.75	1.21	0.000	0.000	2.559	3.559	3.616	0.614	0.444	2.735	0
Ribes uva crispa	0.000	1.162	5	2	14.19	1.17	0.000	0.518	1.566	2.359	2.928	0.700	0.354	1.873	0
Robinia pseudoacacia	2.059	2.059	15	1	37.07	1.79	0.000	0.000	1.063	3.480	3.616	0.808	0.666	2.478	0
Rubus fruticosus agg	2.236	2.236	29	2	62.28	3.49	0.736	1.878	2.236	3.172	3.349	0.930	0.852	3.420	0
Rubus idaeus	1.024	1.024	6	2	21.43	2.04	0.932	0.952	1.717	2.287	2.671	0.938	0.626	2.506	0
Rumex acetosa	0.000	0.000	4	1	39.19	5.49	0.000	0.000	0.000	2.290	2.559	0.838	0.358	1.991	0
Rumex acetosella	0.000	0.099	4	1	12.72	0.97	0.000	0.000	0.000	2.632	2.791	0.766	0.542	2.813	0
Sambucus nigra	0.000	0.000	12	1	34.46	1.39	0.000	0.000	1.043	2.487	3.228	0.810	0.558	2.202	0
Sambucus racemosa	2.288	2.288	5	1	16.13	1.17	0.000	0.928	1.553	2.305	2.377	0.652	0.304	1.765	0
Sorbus aucuparia	0.000	0.000	37	2	69.25	1.64	0.000	0.000	2.154	3.040	3.225	0.562	0.406	1.669	0
Sorbus intermedia	0.000	2.288	4	1	12.90	1.22	0.000	0.000	1.024	2.288	2.377	0.832	0.324	2.156	0
Stellaria media	0.000	0.000	5	2	14.71	0.63	0.000	0.000	1.553	3.349	3.553	0.574	0.368	1.717	0
Ulmus minor	0.000	0.099	5	1	18.52	2.00	0.000	0.000	0.000	2.487	2.669	0.818	0.648	3.270	0
Urtica dioica	0.000	0.000	7	2	20.59	1.14	0.000	0.000	2.125	2.487	2.928	0.676	0.436	1.846	0
Vaccinium myrtillus	0.000	0.000	15	1	37.47	1.92	0.000	0.000	0.863	3.144	3.276	0.848	0.724	2.777	0
Vaccinium vitis idaea	3.172	3.172	4	2	23.51	3.06	0.000	0.000	3.156	3.172	3.223	0.746	0.580	2.978	0
Veronica sublobata	1.024	1.024	10	2	35.71	3.09	0.733	0.825	1.024	1.717	2.559	0.974	0.924	3.370	0

ienv.cp ─ environmental change point for each taxon based on IndVal maximum; **zenv.cp ─** environmental change point for each taxon based on z maximum; **freq ─** number of non-zero abundance values per taxon; **maxgrp ─** 1 if z- (negative response); 2 if z+ (positive response); **IndVal ─** Dufrene and Legendre 1997 IndVal statistic. scaled 0-100%; **zscore ─** IndVal *z* score; **5%, 10%, 50%, 90%, 95% ─** change point quantiles among bootstrap replicates; **purity ─** proportion of replicates matching observed **maxgrp** assignment; reliability ─ proportion of replicate obsiv.prob values < = 0.05; **z.median ─** median score magnitude across all bootstrap replicates; **filter ─** logical (if >0) indicating whether each taxa met purity and reliability criteria. value indicates maxgrp assignment. Abbreviations from Baker et al. (2020).

Table S7. Results of Threshold Indicator Taxa Analysis for *R. pseudoacacia* in nutrient-rich in spring

Species	ienv.cp	zenv.cp	freq	maxgrp	IndVal	Zscore	5%	10%	50%	90%	95%	purity	reliability	z.median	filter
Acer campestre	1.177	1.177	8	1	21.08	1.15	0.000	0.299	1.177	2.841	3.409	0.738	0.370	1.689	0
Acer platanoides	0.000	0.750	15	1	39.20	2.29	0.000	0.000	0.299	2.391	2.977	0.940	0.796	3.087	0
Acer pseudoplatanus	0.299	0.299	26	2	58.78	2.24	0.000	0.299	1.362	2.726	3.516	0.904	0.838	2.769	0
Adoxa moschatellina	0.000	0.000	16	1	52.05	2.42	0.000	0.000	0.299	3.527	3.894	0.438	0.426	1.785	0
Agrostis capillaris	3.916	3.916	9	2	29.07	2.25	0.629	0.815	3.315	4.291	4.335	0.888	0.700	3.018	0
Alliaria petiolata	0.000	0.000	21	1	64.11	3.15	0.000	0.000	1.084	3.916	4.382	0.554	0.490	1.931	0
Anemone nemorosa	0.000	1.362	16	2	34.44	1.84	0.000	0.000	1.362	4.291	4.437	0.908	0.722	2.755	0
Anthriscus sylvestris	3.409	3.409	3	1	8.82	0.31	0.000	0.000	1.747	3.315	3.398	0.250	0.130	1.181	0
Asarum europaeum	2.020	2.020	3	1	11.54	1.34	0.474	0.815	1.362	2.086	2.309	0.590	0.172	1.506	0
Brachypodium sylvaticum	4.135	3.698	14	2	31.84	1.43	0.000	0.000	3.122	4.135	4.479	0.714	0.602	2.334	0
Carex digitata	4.135	4.135	4	2	15.88	1.14	0.000	0.000	2.028	4.135	4.337	0.564	0.422	2.200	0

Carex spicata	3.315	3.315	4	2	26.67	4.62	2.841	3.003	3.315	3.916	4.700	0.982	0.830	5.007	0
Carpinus betulus	3.784	3.170	23	1	52.28	2.39	0.000	0.000	3.170	3.784	3.894	0.872	0.816	2.696	0
Chaerophyllum temulum	3.409	3.409	11	1	28.68	1.36	0.000	0.000	2.391	3.516	3.527	0.596	0.540	2.108	0
Chelidonium majus	0.000	0.000	18	1	78.00	4.55	0.000	0.000	1.084	4.700	4.700	0.690	0.668	2.484	0
Convallaria majalis	4.523	4.523	5	2	22.33	1.95	0.000	0.000	2.447	4.604	4.797	0.538	0.552	2.771	0
Corylus avellana	1.362	1.362	11	2	34.90	2.91	0.750	0.815	1.362	4.325	4.523	0.986	0.914	3.543	0
Crataegus monogyna	0.902	0.750	7	2	19.53	1.22	0.000	0.783	1.084	3.046	3.409	0.642	0.352	1.813	0
Dactylis glomerata	0.000	0.000	16	2	36.82	0.91	0.000	0.000	0.000	3.409	4.182	0.444	0.350	-1.272	0
Dryopteris carthusiana	0.000	0.000	19	2	39.28	1.27	0.000	0.000	2.725	4.382	4.620	0.670	0.482	1.896	0
Dryopteris dilatata	0.000	0.000	3	1	24.90	3.79	0.000	0.000	0.000	4.382	4.620	0.816	0.488	2.810	0
Dryopteris filix mas	0.000	2.391	15	1	33.03	2.00	0.000	0.000	2.420	3.122	3.527	0.616	0.758	2.615	0
Euonymus europaeus	4.700	4.700	11	1	25.58	0.37	0.000	0.000	2.725	4.479	4.523	0.596	0.360	1.384	0
Fagus sylvatica	4.523	1.177	14	2	26.43	0.91	0.000	0.000	2.086	4.342	4.523	0.632	0.520	2.075	0
Fallopia convolvulus	4.382	4.382	23	2	48.95	1.42	0.000	0.000	1.269	4.628	4.945	0.622	0.612	2.343	0
Ficaria verna	0.000	2.841	13	1	28.94	1.45	0.000	0.000	2.020	3.327	3.916	0.642	0.448	1.911	0
Frangula alnus	0.000	0.902	7	2	15.30	0.21	0.000	0.000	1.122	3.264	3.788	0.442	0.292	1.432	0
Fraxinus excelsior	4.700	2.020	21	1	41.90	1.62	0.000	0.000	1.138	3.422	4.025	0.790	0.550	2.045	0
Galeopsis tetrahit	0.000	0.000	24	1	80.90	3.79	0.000	0.000	3.315	4.294	4.700	0.868	0.666	2.631	0
Galium aparine	0.000	0.000	26	1	72.93	3.42	0.000	0.000	0.902	2.731	3.409	0.976	0.918	3.454	0
Geranium robertianum	0.000	1.013	26	1	56.73	1.75	0.000	0.000	0.299	3.420	4.382	0.892	0.712	2.531	0
Geum urbanum	2.020	2.020	16	1	36.43	1.90	0.000	0.000	0.973	3.409	3.516	0.836	0.588	2.214	0
Glechoma hederacea	0.000	0.000	7	1	28.13	1.98	0.000	0.000	1.040	4.700	4.700	0.564	0.558	2.332	0
Hedera helix	0.000	0.000	8	1	56.41	6.50	0.000	0.000	0.000	4.436	4.796	0.834	0.882	4.054	0
Holcus mollis	4.700	4.700	3	2	30.82	2.96	0.000	0.000	4.382	4.700	4.700	0.646	0.586	3.296	0
Hypericum perforatum	0.902	0.973	3	1	15.00	2.36	0.000	0.000	0.902	0.973	1.013	0.940	0.554	2.932	0
Impatiens parviflora	2.020	2.020	41	1	52.79	0.28	0.000	0.000	1.013	4.483	4.796	0.504	0.470	1.899	0
Lactuca muralis	0.000	0.000	18	1	62.04	4.09	0.000	0.000	3.516	4.382	4.479	0.264	0.798	2.990	0
Lamium galeobdolon	2.725	2.725	4	1	13.79	1.12	0.000	0.000	2.020	2.731	2.836	0.616	0.294	1.725	0
Lapsana communis	0.750	0.750	3	2	10.00	0.66	0.000	0.713	2.020	3.252	3.315	0.712	0.128	1.389	0
Lolium giganteum	2.977	2.977	4	2	17.02	2.12	0.000	0.410	2.977	4.604	4.700	0.894	0.566	2.861	0
Luzula pilosa	0.902	0.902	6	1	18.35	1.28	0.000	0.000	0.299	4.118	4.135	0.762	0.604	2.737	0
Maianthemum bifolium	2.841	2.841	10	2	31.65	2.24	0.284	1.050	2.841	3.698	3.790	0.898	0.668	2.559	0
Milium effusum	0.000	0.000	14	1	40.85	2.03	0.000	0.000	3.516	4.335	4.624	0.218	0.638	2.425	0
Moehringia trinervia	1.747	1.747	28	1	51.14	1.74	0.000	0.000	0.967	3.523	4.481	0.804	0.702	2.495	0
Oxalis acetosella	3.698	3.527	8	2	36.05	3.90	2.425	2.725	3.698	4.291	4.291	0.992	0.916	4.730	0
Poa nemoralis	4.523	0.000	27	2	55.12	1.63	0.000	0.000	2.725	4.523	4.523	0.772	0.602	2.164	0
Polygonatum odoratum	3.784	3.784	3	2	16.02	2.17	0.000	0.000	3.698	4.781	4.853	0.666	0.472	3.135	0
Prunus avium	3.698	3.698	10	2	25.20	0.87	0.315	0.750	3.415	3.896	4.701	0.676	0.512	1.970	0
Prunus cerasifera	3.916	3.916	7	1	18.42	0.75	0.000	0.000	1.047	3.516	3.916	0.642	0.292	1.668	0
Prunus domestica	4.700	4.700	6	2	55.68	7.07	2.325	2.391	4.392	4.796	4.813	1.000	0.946	5.942	0
Prunus padus	2.391	1.747	18	2	50.40	3.10	0.782	1.362	2.391	4.291	4.603	0.978	0.924	3.662	0
Prunus serotina	0.000	0.000	26	2	45.09	0.99	0.000	0.000	0.615	3.698	4.291	0.404	0.468	1.896	0
Pteridium aquilinum	3.916	3.916	5	2	28.89	3.36	0.000	0.000	3.894	4.700	4.813	0.830	0.724	3.675	0

Pyrus communis	3.315	3.315	6	2	25.85	2.32	0.331	0.631	3.315	4.479	4.523	0.946	0.656	3.072	0
Quercus petraea	0.000	2.725	24	1	32.69	-0.34	0.000	0.000	0.000	1.747	3.764	0.382	0.480	1.620	0
Quercus robur	1.013	1.013	10	1	27.61	1.80	0.000	0.000	1.013	2.502	2.731	0.876	0.646	2.692	0
Quercus rubra	0.299	0.299	4	1	18.64	2.45	0.000	0.000	0.000	1.362	1.618	0.970	0.696	3.666	0
Ribes uva crispa	0.973	0.902	6	2	20.69	1.77	0.820	0.902	1.013	2.928	3.170	0.884	0.578	2.261	0
Robinia pseudoacacia	0.000	0.000	12	2	33.33	2.02	0.000	0.000	1.362	4.700	4.813	0.566	0.456	1.935	0
Rubus caesius	4.523	4.523	4	2	15.37	1.15	0.000	0.000	0.299	4.523	4.523	0.390	0.626	3.017	0
Rubus fruticosus agg	0.000	0.000	26	2	46.52	0.76	0.000	0.000	1.159	4.291	4.382	0.362	0.468	1.780	0
Rubus idaeus	4.382	2.102	15	2	45.14	3.90	1.355	1.829	2.672	4.382	4.479	0.984	0.940	4.959	0
Sambucus nigra	0.000	0.000	24	2	45.21	1.02	0.000	0.572	3.315	4.717	4.796	0.506	0.460	1.733	0
Sambucus racemosa	0.000	0.000	5	1	37.20	5.43	0.000	0.000	0.000	2.391	2.725	0.966	0.790	4.028	0
Scrophularia nodosa	0.000	0.000	3	1	15.00	1.75	0.000	0.000	0.000	3.252	3.315	0.736	0.372	2.202	0

Abbreviations: see **Table S6**.

Table S8. Results of Threshold Indicator Taxa Analysis for *P. serotina* in nutrient-poor sites in spring

Species	ienv.cp	zenv.cp	freq	maxgrp	IndVal	zscore	5%	10%	50%	90%	95%	Purity	reliability	z.median	filter
Acer platanoides	2.166	2.166	5	2	24.30	2.84	0.000	0.000	2.059	2.167	2.167	0.828	0.548	2.833	0
Acer pseudoplatanus	2.565	2.565	6	2	48.69	4.91	0.763	0.899	2.464	2.664	2.696	0.952	0.842	4.706	0
Agrostis capillaris	0.000	0.000	6	2	17.14	0.66	0.000	0.000	0.647	2.011	2.166	0.472	0.278	1.301	0
Anthoxanthum odoratum	0.000	1.471	12	2	28.41	1.50	0.000	0.000	1.471	2.565	2.696	0.822	0.640	2.489	0
Avenella flexuosa	0.844	0.844	27	2	38.72	0.13	0.000	0.000	2.059	2.696	2.729	0.438	0.356	-1.478	0
Betula pendula	0.000	0.000	13	1	52.17	3.10	0.000	0.000	2.464	2.696	2.696	0.262	0.724	3.165	0
Betula pubescens	1.817	1.128	4	2	13.41	1.01	0.000	0.000	1.416	2.305	2.594	0.820	0.312	1.890	0
Brachypodium sylvaticum	1.563	1.563	3	1	10.00	0.64	0.000	0.000	1.021	1.563	1.592	0.516	0.130	1.340	0
Calamagrostis arundinacea	0.000	0.000	5	1	35.27	3.43	0.000	0.000	0.000	2.565	2.664	0.600	0.750	3.790	0
Calamagrostis epigejos	0.000	0.000	23	2	42.09	0.68	0.083	0.979	2.245	2.630	2.729	0.622	0.356	-1.725	0
Carpinus betulus	0.000	0.553	4	1	16.48	1.71	0.000	0.000	0.553	2.536	2.664	0.814	0.476	2.408	0
Convallaria majalis	0.899	0.899	7	1	18.75	0.86	0.000	0.000	0.899	1.695	1.743	0.740	0.394	1.766	0
Dactylis glomerata	0.647	0.553	5	2	13.78	0.71	0.161	0.647	1.283	2.125	2.464	0.656	0.338	1.684	0
Dryopteris carthusiana	0.000	2.011	29	1	58.59	2.04	0.000	0.000	1.943	2.215	2.305	0.830	0.706	2.397	0
Dryopteris dilatata	1.128	1.128	3	1	12.00	1.59	0.000	0.232	0.824	1.265	1.312	0.744	0.192	1.672	0
Fagus sylvatica	0.553	0.553	7	2	24.14	2.10	0.321	0.404	0.844	2.464	2.565	0.928	0.640	2.558	0
Festuca ovina	1.283	1.128	3	2	8.85	0.44	0.000	0.000	1.283	2.215	2.215	0.704	0.170	1.349	0
Festuca rubra	0.000	0.000	5	1	15.13	0.95	0.000	0.000	0.083	1.592	1.695	0.670	0.334	1.628	0
Frangula alnus	0.000	0.000	17	1	53.77	2.09	0.000	0.000	1.540	2.166	2.245	0.234	0.510	2.039	0
Galeopsis tetrahit	0.658	0.658	4	2	14.81	1.40	0.563	0.652	1.817	2.661	2.729	0.784	0.488	2.362	0
Holcus lanatus	1.817	1.817	3	2	14.05	1.63	0.000	0.000	1.715	1.905	2.011	0.782	0.278	2.011	0
Humulus lupulus	1.695	1.695	3	2	13.25	1.71	0.000	0.000	1.665	1.905	2.011	0.784	0.256	1.932	0
Hypericum perforatum	0.000	0.000	4	2	11.43	0.40	0.000	0.000	0.763	2.011	2.011	0.396	0.238	1.478	0
Impatiens parviflora	2.565	2.565	6	2	44.34	4.45	0.000	0.743	2.464	2.696	2.696	0.868	0.764	4.407	0

Lactuca muralis	2.011	1.817	9	2	28.18	2.02	0.414	0.652	1.817	2.464	2.565	0.850	0.658	2.828	0
Lysimachia europaea	0.083	0.083	3	1	18.75	3.40	0.000	0.000	0.000	0.083	0.236	0.952	0.728	4.438	0
Maianthemum bifolium	0.000	0.000	4	1	46.42	7.35	0.000	0.000	0.000	0.166	0.321	0.990	0.870	5.147	0
Melampyrum pratense	2.565	0.000	13	2	28.81	1.01	0.000	0.000	0.743	2.011	2.305	0.538	0.540	2.063	0
Moehringia trinervia	0.000	0.000	12	2	30.00	0.95	0.000	0.000	0.652	2.014	2.260	0.730	0.448	1.872	0
Pilosella officinarum	0.083	1.817	6	2	18.69	1.46	0.000	0.083	1.283	2.059	2.166	0.920	0.520	2.250	0
Pinus sylvestris	2.565	2.305	23	2	68.6	4.02	0.743	1.692	2.305	2.600	2.600	0.914	0.880	3.847	0
Poa nemoralis	2.565	2.565	4	2	29.77	3.99	0.652	0.738	2.275	2.565	2.696	0.856	0.580	2.872	0
Prunus cerasifera	2.629	2.629	3	2	18.67	1.75	0.000	0.000	0.971	2.729	2.741	0.494	0.554	3.228	0
Prunus domestica	2.166	2.166	3	1	8.33	0.04	0.000	0.000	1.151	1.992	2.011	0.470	0.146	1.508	0
Prunus padus	2.245	2.245	4	2	19.46	1.62	0.000	0.000	2.167	2.405	2.565	0.738	0.448	2.569	0
Prunus serotina	0.000	0.000	40	2	67.18	0.78	0.000	0.000	0.000	2.305	2.629	0.334	0.414	1.779	0
Pyrus communis	2.565	2.565	3	2	24.40	3.28	0.000	0.000	2.305	2.565	2.696	0.600	0.570	2.919	0
Quercus petraea	2.629	2.565	36	1	62.61	1.16	0.000	0.000	1.680	2.696	2.729	0.626	0.588	2.096	0
Quercus robur	2.565	2.565	9	2	56.28	5.62	0.000	1.509	2.245	2.696	2.696	0.900	0.924	5.259	0
Quercus rubra	2.436	2.436	6	2	23.61	1.69	0.000	0.000	1.577	2.436	2.504	0.752	0.478	2.301	0
Rubus fruticosus agg	0.000	0.000	26	1	43.45	0.11	0.000	0.000	0.000	1.743	2.306	0.570	0.392	1.355	0
Rubus idaeus	0.743	0.743	10	1	24.64	1.10	0.000	0.000	0.743	1.887	2.065	0.780	0.424	1.864	0
Rumex acetosella	0.000	0.000	11	2	29.51	1.74	0.000	0.083	1.552	2.274	2.594	0.858	0.594	2.305	0
Sorbus aucuparia	2.629	0.658	38	1	52.83	0.77	0.000	0.000	0.738	2.600	2.696	0.564	0.472	1.879	0
Stellaria media	2.011	2.011	9	2	31.22	2.23	0.000	0.658	1.943	2.664	2.696	0.918	0.736	2.940	0
Vaccinium myrtillus	0.000	0.000	28	1	77.63	3.64	0.000	0.000	1.105	2.248	2.662	0.868	0.776	3.040	0
Vaccinium vitis idaea	1.563	1.563	6	1	16.31	0.77	0.000	0.000	0.844	1.592	1.621	0.606	0.312	1.593	0

Abbreviations: see **Table S6**.

Table S9. Results of Threshold Indicator Taxa Analysis for *P. serotina* in nutrient-rich sites in spring

Species	ienv.cp	zenv.cp	freq	maxgrp	IndVal	zscore	5%	10%	50%	90%	95%	purity	reliability	z.median	filter
Acer campestre	0.000	0.000	3	1	26.32	4.93	0.000	0.000	0.000	1.522	1.57	0.766	0.314	2.124	0
Acer platanoides	1.135	1.135	8	2	20.16	0.66	0.000	0.000	1.258	2.687	2.892	0.552	0.432	1.680	0
Acer pseudoplatanus	2.718	2.718	24	2	51.91	1.05	0.000	0.000	1.062	2.718	2.788	0.658	0.632	2.237	0
Adoxa moschatellina	0.000	0.000	10	1	47.99	3.75	0.000	0.000	1.552	2.753	2.935	0.276	0.578	2.379	0
Agrostis capillaris	0.000	1.002	9	1	39.13	4.24	0.283	0.332	1.002	1.075	1.135	0.998	0.992	4.959	1
Alliaria petiolata	2.718	2.718	22	2	41.91	0.26	0.000	0.078	1.859	2.931	3.001	0.480	0.596	2.275	0
Allium schoenoprasum	1.599	1.072	4	2	16.67	2.63	1.060	1.075	1.582	2.823	3.001	0.968	0.646	3.135	0
Anemone nemorosa	2.718	0.759	12	2	21.4	0.36	0.000	0.000	0.828	2.897	3.001	0.676	0.504	1.982	0
Anthoxanthum odoratum	0.000	0.000	3	1	14.38	1.23	0.000	0.000	0.283	2.200	2.200	0.534	0.268	1.937	0
Anthriscus sylvestris	0.000	0.000	3	1	33.31	5.16	0.000	0.000	0.000	1.062	1.066	0.934	0.454	2.559	0
Athyrium filix femina	0.472	0.405	3	2	10.71	1.08	0.186	0.431	1.073	2.892	3.001	0.604	0.282	1.708	0
Avenella flexuosa	2.088	2.088	4	2	17.69	1.47	0.087	0.087	1.423	2.088	2.109	0.770	0.358	1.917	0
Brachypodium sylvaticum	2.088	1.944	20	2	50.29	2.92	0.000	0.087	1.944	2.124	2.167	0.900	0.776	3.161	0

Calamagrostis arundinacea	0.000	0.000	6	2	15.38	0.56	0.000	0.000	1.458	1.944	1.980	0.654	0.366	1.671	0
Calamagrostis epigejos	0.000	0.000	5	2	14.71	0.8	0.087	0.255	1.423	2.279	2.279	0.712	0.278	1.416	0
Carex digitata	0.000	1.944	4	2	13.98	1.12	0.000	0.000	1.774	2.124	2.200	0.588	0.398	2.050	0
Carex pilulifera	1.458	1.458	3	1	10.34	1.03	0.000	0.000	0.458	1.458	1.487	0.762	0.184	1.503	0
Carex spicata	0.000	1.701	9	1	27.27	2.37	0.000	0.247	1.075	1.745	1.790	0.950	0.698	2.960	0
Carpinus betulus	1.522	1.522	19	2	59.22	4.2	0.083	1.280	1.522	1.701	2.508	0.958	0.924	4.555	0
Chaerophyllum temulum	2.718	2.718	9	2	54.5	4.36	0.000	0.000	2.373	3.001	3.001	0.886	0.754	4.209	0
Chelidonium majus	2.279	2.279	7	2	23.56	1.22	0.000	0.000	1.599	2.279	2.718	0.706	0.486	2.042	0
Convallaria majalis	1.970	1.970	9	1	21.53	0.59	0.000	0.000	0.000	1.835	1.945	0.744	0.372	1.634	0
Corylus avellana	2.718	2.718	8	2	76.41	7.74	1.900	2.011	2.279	2.892	3.001	0.990	0.962	8.144	2
Crataegus monogyna	2.718	2.718	6	2	19.17	0.73	0.000	0.000	1.570	2.931	3.110	0.582	0.402	1.813	0
Crataegus rhipidophylla	1.996	1.996	6	2	17.86	1.15	0.000	0.000	1.531	2.012	2.823	0.686	0.398	2.068	0
Dactylis glomerata	1.970	1.970	18	1	37.75	0.82	0.000	0.000	0.759	1.970	1.980	0.444	0.386	1.626	0
Dryopteris carthusiana	1.002	1.002	21	1	35.04	0.88	0.000	0.000	0.425	2.124	2.753	0.690	0.494	1.889	0
Dryopteris dilatata	0.000	0.000	3	2	7.89	0.05	0.000	0.000	1.002	1.961	1.970	0.406	0.250	1.633	0
Dryopteris filix mas	2.718	2.718	14	2	40.13	1.52	0.083	0.364	1.552	2.823	2.892	0.904	0.706	2.760	0
Euonymus europaeus	2.279	2.279	8	2	30.3	1.94	0.196	0.283	1.835	2.718	2.718	0.868	0.710	2.937	0
Fagus sylvatica	1.970	1.970	19	2	48.4	2.65	0.000	0.000	1.954	2.062	2.462	0.798	0.790	3.170	0
Fallopia convolvulus	1.970	1.970	23	1	47.32	1.65	0.000	0.000	1.599	1.970	1.986	0.822	0.586	2.225	0
Festuca ovina	0.000	0.000	3	1	22.59	2.38	0.000	0.000	0.174	2.200	2.200	0.418	0.392	2.279	0
Ficaria verna	0.000	0.000	4	1	18.02	1.13	0.000	0.000	1.187	2.938	3.110	0.412	0.398	2.130	0
Fragaria vesca	0.364	1.458	4	1	13.79	1.56	0.196	0.283	0.759	1.458	1.487	0.548	0.372	2.013	0
Frangula alnus	0.000	0.000	7	1	29.66	2.27	0.000	0.000	0.405	1.944	2.012	0.632	0.428	1.973	0
Fraxinus excelsior	2.718	2.718	16	2	56.26	2.55	0.000	1.072	1.996	2.718	2.718	0.934	0.830	3.398	0
Galeopsis tetrahit	2.718	2.718	21	2	55.78	1.92	0.000	0.000	1.135	2.718	2.718	0.556	0.680	2.362	0
Galium aparine	0.000	0.000	27	1	85.69	3.72	0.000	0.000	0.087	2.279	2.718	0.788	0.660	2.508	0
Geranium robertianum	0.000	1.329	30	1	56.58	1.26	0.000	0.000	1.280	2.241	2.718	0.770	0.578	2.078	0
Geum urbanum	2.718	2.718	14	2	62.56	3.92	0.000	0.000	1.991	2.788	3.001	0.872	0.836	3.678	0
Glechoma hederacea	0.000	0.000	4	1	32.5	5.22	0.000	0.000	0.000	1.423	1.970	0.886	0.586	3.353	0
Hedera helix	1.904	1.904	7	2	21.97	1.14	0.000	0.000	1.136	1.904	1.929	0.716	0.436	1.904	0
Hieracium murorum	2.200	2.200	3	2	11.9	0.69	0.000	0.000	1.458	2.200	2.200	0.674	0.280	1.858	0
Humulus lupulus	2.279	2.279	4	2	28.45	2.97	0.000	0.000	2.200	2.464	2.718	0.808	0.646	3.667	0
Hypericum perforatum	0.405	0.405	3	2	10.71	1.13	0.209	0.378	1.235	1.522	1.570	0.604	0.168	1.455	0
Impatiens parviflora	0.000	1.329	36	1	51.53	1.18	0.000	0.283	1.582	2.569	2.718	0.666	0.590	2.237	0
Juncus effusus	0.472	0.472	7	1	27.56	3.22	0.000	0.000	0.472	0.765	1.002	0.982	0.804	3.621	0
Lactuca muralis	2.279	1.187	26	1	54.01	2.96	0.000	0.000	1.187	2.279	2.327	0.978	0.872	3.351	0
Lamium galeobdolon	0.000	0.000	4	1	18.70	2.78	0.000	0.000	0.000	0.572	1.600	0.924	0.672	3.428	0
Lapsana communis	2.718	2.718	3	2	19.44	1.55	0.000	0.000	1.975	2.892	3.001	0.684	0.308	2.208	0
Lolium giganteum	0.000	0.000	10	1	24.30	0.78	0.000	0.000	1.183	2.279	2.279	0.600	0.444	1.895	0
Luzula pilosa	0.000	0.000	7	1	19.16	0.4	0.000	0.000	0.759	2.072	2.088	0.636	0.412	1.785	0
Maianthemum bifolium	0.000	0.000	11	1	29.36	1.78	0.000	0.000	0.000	1.184	1.458	0.852	0.584	2.364	0
Melica nutans	1.522	0.472	6	1	18.83	2.05	0.000	0.000	0.472	1.540	1.552	0.924	0.652	2.842	0
Melica uniflora	0.000	0.000	4	2	10.81	0.23	0.000	0.000	0.472	2.753	2.892	0.374	0.242	1.496	0

Milium effusum	0.000	0.000	11	1	33.85	1.26	0.000	0.000	0.759	1.944	1.954	0.786	0.468	1.878	0
Moehringia trinervia	2.200	1.701	31	1	47.81	0.9	0.000	0.000	1.062	1.996	2.200	0.720	0.544	2.083	0
Oxalis acetosella	1.458	1.458	6	1	20.69	1.72	0.000	0.000	0.759	1.488	1.522	0.920	0.554	2.321	0
Poa nemoralis	2.088	2.088	32	2	50.17	0.47	0.000	0.000	0.283	2.099	2.503	0.760	0.574	2.175	0
Polygonatum odoratum	0.000	0.000	5	1	36.86	5.03	0.000	0.000	0.000	1.075	1.620	0.896	0.586	2.85	0
Prunus avium	0.174	0.174	5	2	16.13	1.34	0.087	0.174	1.329	2.892	3.110	0.758	0.386	1.954	0
Prunus cerasifera	2.088	2.088	6	1	15.38	0.41	0.000	0.000	1.329	1.996	2.012	0.376	0.274	1.219	0
Prunus domestica	1.187	1.187	4	1	15.38	1.82	0.000	0.000	1.138	1.285	1.345	0.734	0.334	1.879	0
Prunus padus	0.000	1.599	10	2	24.51	1.43	0.000	0.000	1.835	3.001	3.110	0.728	0.648	2.713	0
Prunus serotina	2.503	1.599	33	1	62.00	1.61	0.000	0.000	1.280	1.835	2.047	0.774	0.558	1.962	0

Abbreviations: see **Table S6**.

Table S10. Results of Threshold Indicator Taxa Analysis for *R. pseudoacacia* in nutrient-poor sites in summer

Species	ienv.cp	zenv.cp	freq	maxgrp	IndVal	zscore	5%	10%	50%	90%	95%	purity	reliability	z.median	filter
Acer platanoides	1.063	1.024	9	2	32.14	2.92	0.935	1.024	1.336	3.349	3.349	0.994	0.928	3.725	0
Acer pseudoplatanus	1.958	1.958	7	2	27.12	2.45	1.336	1.576	1.958	2.559	2.743	0.964	0.804	3.152	0
Agrostis capillaris	2.791	2.791	9	2	22.01	0.92	0.000	0.000	2.305	3.144	3.228	0.636	0.508	1.936	0
Alliaria petiolata	3.172	3.156	4	2	32.91	6.15	2.059	2.142	3.159	3.223	3.298	0.978	0.794	5.451	0
Amelanchier spicata	3.172	3.172	3	2	24.19	3.18	1.844	2.069	3.156	3.484	3.553	0.962	0.614	3.888	0
Anthoxanthum odoratum	0.000	0.000	3	1	17.67	3.00	0.000	0.000	0.000	2.170	2.203	0.828	0.322	2.117	0
Arrhenatherum elatius	3.092	3.092	3	2	19.67	3.20	1.815	2.069	2.980	3.547	3.616	0.952	0.596	3.262	0
Avenella flexuosa	0.736	0.736	26	1	54.27	2.39	0.000	0.000	0.736	3.144	3.349	0.890	0.722	2.708	0
Betula pendula	2.059	2.059	7	1	21.74	1.16	0.000	0.000	0.974	2.092	2.203	0.666	0.454	1.889	0
Calamagrostis epigejos	2.170	2.170	23	2	54.98	3.25	0.000	0.404	2.170	2.372	2.742	0.968	0.890	3.764	0
Carpinus betulus	2.059	2.059	5	1	13.98	0.48	0.000	0.404	1.958	3.553	3.752	0.438	0.284	1.544	0
Chelidonium majus	2.559	2.271	12	2	56.42	7.05	1.958	2.059	2.269	2.583	2.928	1.000	1.000	7.378	2
Convallaria majalis	3.484	3.484	5	2	22.98	1.82	0.000	0.923	3.172	3.811	3.880	0.764	0.488	2.350	0
Crataegus rhipidophylla	3.484	2.377	3	2	11.11	0.98	0.305	0.724	2.377	3.547	3.616	0.810	0.340	2.049	0
Dactylis glomerata	0.404	0.404	5	2	12.59	0.32	0.000	0.404	1.162	3.210	3.225	0.506	0.242	1.404	0
Dryopteris carthusiana	0.935	1.717	25	2	64.30	4.94	0.603	0.809	1.118	1.740	1.851	0.984	0.994	4.954	2
Dryopteris dilatata	2.559	1.118	4	2	15.38	2.39	1.265	1.500	2.237	2.791	2.791	0.962	0.598	3.019	0
Dryopteris filix mas	0.404	0.404	3	2	9.680	0.55	0.099	0.305	1.063	2.956	3.092	0.338	0.176	1.441	0
Fagus sylvatica	0.000	0.000	4	1	15.62	1.23	0.000	0.000	1.040	2.559	2.693	0.656	0.230	1.578	0
Fallopia convolvulus	1.717	1.717	14	2	60.87	7.59	1.162	1.336	1.717	3.093	3.364	1.000	1.000	7.229	2
Festuca ovina	3.484	3.484	5	2	17.81	0.61	0.000	0.000	2.377	3.811	4.076	0.592	0.434	2.100	0
Festuca rubra	3.484	3.484	4	2	18.54	1.18	0.000	0.000	2.449	3.880	4.076	0.650	0.428	2.243	0
Frangula alnus	3.484	3.484	29	1	56.92	0.95	0.000	0.000	1.118	3.172	3.411	0.652	0.412	1.794	0
Fraxinus excelsior	3.484	0.935	4	2	13.79	1.43	0.861	0.952	2.203	3.685	3.880	0.850	0.402	2.161	0
Galeopsis tetrahit	0.404	0.404	10	2	32.26	2.27	0.199	0.305	1.162	3.092	3.105	0.974	0.810	2.909	0
Geranium robertianum	1.336	1.336	12	2	42.68	4.48	0.305	0.404	1.336	3.144	3.172	0.996	0.986	4.761	2

Hedera helix	3.172	3.156	3	2	20.69	3.58	1.084	1.270	3.159	3.616	3.880	0.920	0.564	3.592	0
Humulus lupulus	0.404	0.099	6	2	18.75	1.33	0.305	0.404	1.686	2.583	2.693	0.718	0.432	1.862	0
Impatiens parviflora	1.717	1.717	16	2	56.35	5.59	0.305	0.305	1.655	2.271	2.791	0.998	1.000	5.403	2
Lactuca muralis	0.404	0.404	6	2	19.35	1.75	0.305	0.305	2.059	3.172	3.172	0.850	0.590	2.373	0
Maianthemum bifolium	1.958	1.958	3	2	8.67	0.40	0.000	0.000	1.958	2.693	2.717	0.654	0.194	1.440	0
Melampyrum pratense	0.000	0.000	12	1	62.39	7.08	0.000	0.000	0.099	1.162	1.542	0.998	0.994	6.630	1
Moehringia trinervia	1.336	1.162	20	2	75.31	8.54	1.118	1.162	1.500	2.059	2.059	1.000	1.000	8.243	2
Pinus sylvestris	0.000	0.000	14	1	65.39	7.32	0.000	0.000	0.991	1.079	1.106	1.000	0.998	6.988	1
Poa nemoralis	2.271	2.236	4	2	21.05	3.13	2.127	2.205	2.583	3.547	3.685	0.988	0.780	4.112	0
Prunus avium	1.717	1.717	5	2	21.74	2.69	1.172	1.486	1.717	2.958	3.092	0.978	0.736	3.262	0
Prunus cerasifera	0.000	0.000	9	2	26.47	1.99	0.000	0.305	1.118	3.298	3.553	0.876	0.570	2.347	0
Prunus padus	2.928	2.928	4	2	27.19	3.28	2.091	2.138	2.904	3.156	3.547	0.978	0.782	4.390	0
Prunus serotina	1.162	1.336	32	2	51.69	0.73	0.000	0.404	2.170	3.411	3.484	0.500	0.428	1.772	0
Pteridium aquilinum	0.000	2.693	3	1	8.82	0.57	0.000	0.000	1.024	2.377	2.559	0.624	0.220	1.491	0
Pyrus communis	3.225	1.958	4	2	18.18	3.12	1.464	1.577	2.203	3.237	3.688	0.964	0.662	3.378	0
Quercus petraea	3.484	1.717	42	1	84.61	4.51	1.024	1.129	1.336	2.170	2.271	1.000	1.000	4.671	1
Quercus robur	0.000	0.000	6	1	19.55	0.84	0.000	0.000	1.969	3.225	3.225	0.516	0.358	1.517	0
Quercus rubra	0.000	0.000	7	1	32.46	3.52	0.000	0.000	0.404	1.510	3.298	0.926	0.850	4.053	0
Ribes uva crispa	2.236	2.236	6	2	18.32	1.39	0.000	0.000	2.205	2.993	3.211	0.706	0.392	1.848	0
Robinia pseudoacacia	0.099	0.736	32	2	87.97	6.13	0.000	0.099	0.404	1.934	2.094	1.000	1.000	6.057	2
Rubus fruticosus agg	1.024	1.118	28	2	80.80	8.15	0.305	0.610	1.063	1.471	1.566	1.000	1.000	8.364	2
Rubus idaeus	1.717	0.404	8	2	22.56	1.43	0.099	0.305	1.717	2.956	3.092	0.872	0.586	2.210	0
Rumex acetosa	2.059	2.059	3	2	14.29	1.99	1.491	1.717	2.059	2.742	2.742	0.906	0.404	2.362	0
Rumex acetosella	0.000	0.000	5	1	19.68	2.07	0.000	0.000	0.000	2.236	2.271	0.954	0.690	3.074	0
Sambucus nigra	3.172	2.928	8	2	44.54	5.48	2.518	2.663	2.928	3.172	3.223	1.000	0.978	6.064	2
Sorbus aucuparia	1.162	1.162	30	2	53.55	1.55	0.000	0.000	1.162	3.223	3.547	0.810	0.640	2.332	0
Stellaria media	3.092	2.928	3	2	18.01	2.78	1.533	1.740	2.975	3.223	3.225	0.948	0.510	2.942	0
Ulmus minor	2.271	2.271	7	2	31.86	3.30	0.952	1.024	2.271	2.377	2.487	0.986	0.846	3.749	0
Urtica dioica	1.024	1.024	5	2	17.86	1.61	0.825	0.952	1.500	2.310	2.719	0.752	0.436	1.996	0
Vaccinium myrtillus	0.000	0.000	14	1	67.29	6.38	0.000	0.000	0.149	2.059	2.059	1.000	0.994	6.595	1
Vaccinium vitis idaea	1.162	1.162	4	1	17.39	2.38	0.000	0.000	0.000	1.325	1.543	0.948	0.678	3.499	0

Abbreviations: see **Table S6**.

Table S11. Results of Threshold Indicator Taxa Analysis for *R. pseudoacacia* in nutrient-rich sites in summer

Species	ienv.cp	zenv.cp	freq	maxgrp	IndVal	zscore	5%	10%	50%	90%	95%	purity	reliability	z.median	filter
Acer campestre	2.841	2.841	11	2	36.08	3.20	0.631	0.631	2.841	3.916	4.291	0.988	0.888	3.655	0
Acer platanoides	3.916	3.916	14	2	44.67	2.80	0.973	2.095	3.315	4.335	4.525	0.944	0.788	3.419	0
Acer pseudoplatanus	0.000	1.013	28	2	44.22	0.55	0.000	1.013	3.315	4.796	4.945	0.524	0.494	1.765	0
Agrostis capillaris	4.700	4.700	3	2	18.74	1.21	0.000	0.000	0.647	4.813	4.945	0.476	0.550	3.298	0
Alliaria petiolata	4.523	4.523	11	2	35.34	1.95	0.000	0.000	3.315	4.479	4.523	0.634	0.666	2.974	0

Anemone nemorosa	0.000	0.000	4	1	27.42	4.22	0.000	0.000	0.000	4.813	4.945	0.710	0.706	3.784	0
Asarum europaeum	3.698	3.698	3	2	15.00	2.03	0.000	0.000	3.592	4.337	4.382	0.698	0.458	2.778	0
Avenella flexuosa	0.750	0.750	4	1	16.43	1.77	0.000	0.000	0.750	2.725	2.841	0.908	0.452	2.239	0
Brachypodium sylvaticum	0.000	0.000	14	1	48.12	3.12	0.000	0.000	0.000	3.527	3.592	0.890	0.782	3.117	0
Calamagrostis epigejos	0.299	0.299	6	1	31.23	4.92	0.000	0.000	0.000	0.331	0.600	0.990	0.920	5.075	0
Carex spicata	0.299	0.299	5	1	23.05	3.68	0.000	0.000	0.000	4.700	4.796	0.844	0.830	4.292	0
Carpinus betulus	0.000	0.000	18	1	50.88	2.95	0.000	0.000	0.000	1.850	3.316	0.896	0.708	2.621	0
Chaerophyllum temulum	3.409	3.409	14	2	32.86	1.90	0.000	0.000	3.398	4.291	4.560	0.666	0.614	2.374	0
Chelidonium majus	0.000	0.299	20	2	56.77	3.91	0.000	0.000	0.299	3.127	3.527	0.984	0.958	3.778	2
Circaea lutetiana	0.000	2.391	7	1	16.75	0.73	0.000	0.000	0.973	3.315	4.435	0.650	0.376	1.729	0
Convallaria majalis	3.315	3.315	5	1	15.15	1.00	0.000	0.000	0.299	3.170	3.315	0.658	0.382	1.762	0
Corylus avellana	4.700	0.973	13	2	42.10	3.07	0.837	0.908	3.034	4.945	4.945	0.974	0.948	4.685	0
Crataegus rhipidophylla	0.000	0.000	6	1	29.60	2.31	0.000	0.000	0.902	4.337	4.382	0.552	0.400	1.789	0
Dactylis glomerata	2.020	2.020	10	2	25.23	0.97	0.000	0.000	2.020	3.422	3.592	0.692	0.380	1.648	0
Dryopteris carthusiana	3.784	0.902	24	2	53.93	3.16	0.663	0.815	1.177	4.003	4.182	0.990	0.958	4.099	2
Dryopteris dilatata	0.902	0.902	5	2	17.24	1.86	0.783	0.837	1.747	4.779	4.815	0.888	0.488	2.284	0
Dryopteris filix mas	0.000	1.747	14	2	29.39	1.43	0.000	0.783	2.725	4.928	4.945	0.896	0.688	2.652	0
Euonymus europaeus	0.000	0.973	12	2	33.67	2.41	0.299	0.331	0.973	4.291	4.384	0.946	0.790	2.907	0
Fagus sylvatica	2.102	2.102	19	1	38.07	1.16	0.000	0.000	2.102	4.717	4.813	0.538	0.524	1.972	0
Fallopia convolvulus	4.700	2.102	28	2	43.40	1.35	0.000	0.000	1.205	4.603	4.700	0.826	0.602	2.359	0
Fragaria vesca	2.725	2.725	3	2	10.36	0.96	0.000	0.000	2.502	3.327	3.409	0.808	0.192	1.446	0
Frangula alnus	1.177	1.177	8	2	25.98	1.96	1.006	1.084	1.177	4.135	4.603	0.934	0.734	3.047	0
Fraxinus excelsior	4.700	2.102	23	2	50.72	1.86	0.902	1.140	2.436	4.700	4.701	0.744	0.768	2.535	0
Galeopsis tetrahit	0.000	0.000	22	1	53.50	2.48	0.000	0.000	0.631	3.698	3.763	0.920	0.762	2.768	0
Geranium robertianum	0.000	3.409	25	2	56.50	2.93	0.000	0.783	3.041	3.916	4.700	0.970	0.862	3.527	0
Geum urbanum	0.973	0.973	17	2	41.58	1.71	0.000	0.908	2.086	3.763	4.291	0.906	0.688	2.477	0
Glechoma hederacea	4.700	0.000	5	2	14.29	0.89	0.000	0.000	1.269	4.813	4.928	0.648	0.376	1.835	0
Hedera helix	0.000	1.084	13	1	28.49	1.00	0.000	0.000	0.299	3.527	4.603	0.796	0.550	2.085	0
Humulus lupulus	3.784	2.102	5	2	23.81	3.26	1.747	2.020	2.725	4.182	4.291	0.982	0.796	3.771	0
Hypericum perforatum	0.000	0.000	4	1	28.45	3.70	0.000	0.000	0.299	0.822	0.902	0.986	0.764	3.973	0
Impatiens parviflora	0.000	3.170	43	2	63.94	3.05	0.000	0.000	3.040	3.527	4.435	0.904	0.826	2.978	0
Juncus effusus	0.000	0.000	3	1	14.57	1.51	0.000	0.000	0.000	3.784	3.784	0.658	0.382	2.433	0
Lactuca muralis	1.013	1.013	19	1	42.83	2.05	0.000	0.000	1.013	4.291	4.779	0.770	0.712	2.806	0
Lamium galeobdolon	3.916	3.916	6	2	28.93	3.01	0.000	0.000	3.830	4.249	4.291	0.838	0.672	3.067	0
Lolium giganteum	3.409	3.409	3	2	13.66	1.82	0.000	0.908	3.398	4.813	4.929	0.868	0.374	2.382	0
Luzula pilosa	0.299	0.299	3	1	18.75	3.73	0.000	0.000	0.000	0.331	0.599	0.946	0.628	4.019	0
Maianthemum bifolium	4.700	4.523	8	2	31.62	2.52	0.000	0.299	4.291	4.928	4.945	0.868	0.698	3.204	0
Melampyrum pratense	0.000	0.000	3	1	10.13	0.39	0.000	0.000	0.331	4.135	4.135	0.482	0.368	2.167	0
Melica nutans	4.291	4.291	3	2	22.73	3.54	0.000	0.000	4.116	4.291	4.335	0.692	0.430	3.213	0
Milium effusum	2.102	2.102	5	1	18.52	1.91	0.000	0.000	2.053	2.436	2.571	0.886	0.428	2.062	0
Moehringia trinervia	1.177	1.747	22	2	38.06	1.43	0.000	0.000	1.177	3.838	4.293	0.784	0.608	2.333	0
Oxalis acetosella	4.700	0.000	8	1	32.41	2.06	0.000	0.000	0.375	4.945	5.077	0.550	0.908	4.062	0
Pinus sylvestris	0.000	0.631	5	1	13.28	0.61	0.000	0.000	0.718	4.779	4.796	0.646	0.522	2.355	0

Poa nemoralis	0.000	0.000	24	1	57.49	2.63	0.000	0.000	3.233	4.700	4.700	0.764	0.614	2.281	0
Prunus avium	2.020	2.020	15	1	36.68	1.20	0.000	0.000	1.047	2.102	3.320	0.644	0.574	2.023	0
Prunus cerasifera	3.784	2.102	11	2	28.23	1.75	0.000	0.000	2.102	4.028	4.135	0.848	0.626	2.432	0
Prunus domestica	0.000	0.000	5	1	13.64	0.52	0.000	0.000	0.782	4.335	4.382	0.594	0.366	1.943	0
Prunus padus	0.299	0.299	18	2	48.34	2.99	0.000	0.000	0.734	4.928	4.945	0.944	0.934	3.413	0
Prunus serotina	4.700	4.700	21	2	73.23	3.77	0.000	0.631	4.382	4.700	4.717	0.954	0.848	3.762	0
Pteridium aquilinum	0.000	0.000	5	1	33.33	5.13	0.000	0.000	0.000	0.331	0.599	0.998	0.936	5.736	0
Pyrus communis	4.291	4.291	5	1	12.50	0.12	0.000	0.000	1.563	3.269	3.527	0.534	0.196	1.265	0
Quercus petraea	1.362	1.177	34	1	82.81	3.19	0.000	0.000	1.122	1.563	1.703	0.986	0.956	3.479	1
Quercus robur	3.409	1.362	10	2	36.29	3.90	1.177	1.306	2.841	4.194	4.291	1.000	0.974	4.814	2
Quercus rubra	4.700	0.902	10	2	24.83	0.96	0.000	0.663	2.168	4.700	4.700	0.692	0.476	1.960	0
Ribes uva crispa	3.916	3.916	4	2	16.40	1.61	0.629	0.815	3.106	4.335	4.382	0.770	0.428	2.163	0
Robinia pseudoacacia	0.000	0.299	27	2	71.84	4.98	0.000	0.000	0.299	1.105	2.102	0.998	0.988	5.283	2
Rubus caesius	0.000	0.000	11	2	27.67	1.12	0.000	0.000	2.086	4.135	4.335	0.694	0.586	2.386	0
Rubus fruticosus agg	4.382	4.382	20	1	38.34	0.58	0.000	0.000	0.973	3.916	4.324	0.626	0.414	1.698	0
Rubus idaeus	4.135	2.725	16	2	30.51	0.80	0.000	0.000	2.502	4.386	4.815	0.574	0.666	2.509	0
Sambucus nigra	0.902	0.902	23	2	49.78	1.37	0.000	0.299	1.763	4.291	4.335	0.852	0.680	2.325	0
Sorbus aucuparia	0.000	0.000	8	2	21.05	0.88	0.000	0.000	2.841	4.813	4.945	0.372	0.512	2.190	0

Abbreviations: see **Table S6**.

Table S12. Results of Threshold Indicator Taxa Analysis for *P. serotina* in nutrient-poor sites in summer

Species	ienv.cp	zenv.cp	freq	maxgrp	IndVal	zscore	5%	10%	50%	90%	95%	purity	reliability	z.median	filter
Acer platanoides	1.817	1.593	3	2	11.64	1.52	0.000	0.799	1.593	1.998	2.245	0.902	0.386	2.209	0
Acer pseudoplatanus	2.629	2.629	7	2	34.77	2.35	0.404	0.553	1.992	2.629	2.629	0.942	0.702	3.146	0
Agrostis capillaris	1.593	1.593	14	2	38.65	2.17	0.000	0.232	1.593	1.768	2.244	0.844	0.666	2.545	0
Anthoxanthum odoratum	1.593	1.593	11	2	39.30	3.47	0.232	0.315	1.593	2.122	2.166	0.954	0.810	3.212	0
Avenella flexuosa	2.565	2.436	34	1	77.77	2.78	0.000	1.021	1.593	2.499	2.565	0.920	0.928	3.236	0
Betula pendula	0.000	0.000	17	2	40.97	1.80	0.000	0.083	0.414	1.665	2.248	0.600	0.774	2.673	0
Calamagrostis arundinacea	2.436	2.436	6	2	32.05	2.94	0.743	0.763	1.117	2.436	2.594	0.968	0.800	3.391	0
Calamagrostis epigejos	0.000	0.743	25	2	40.67	0.39	0.000	0.000	0.647	2.166	2.166	0.686	0.442	1.621	0
Carpinus betulus	2.629	1.563	3	2	10.88	0.88	0.000	0.000	1.541	2.6	2.629	0.724	0.282	1.996	0
Convallaria majalis	2.166	2.166	5	2	17.22	1.46	0.083	0.315	1.991	2.335	2.436	0.746	0.382	1.713	0
Dactylis glomerata	1.593	1.593	3	2	12.41	1.16	0.000	0.000	1.593	2.305	2.305	0.830	0.364	2.110	0
Dryopteris carthusiana	0.647	0.647	29	2	75.56	5.92	0.232	0.315	0.647	1.021	1.695	1.000	1.000	6.269	2
Fagus sylvatica	2.245	2.245	9	2	49.67	4.72	1.283	1.416	2.244	2.629	2.662	0.992	0.954	5.499	2
Fallopia convolvulus	2.245	1.817	3	2	21.43	3.78	0.000	1.593	1.817	2.245	2.245	0.946	0.694	4.360	0
Frangula alnus	2.305	2.305	30	1	51.19	0.94	0.000	0.000	0.899	2.305	2.305	0.442	0.504	2.010	0
Galeopsis tetrahit	2.245	2.245	3	2	20.60	2.47	0.461	0.647	2.216	2.274	2.275	0.844	0.466	2.810	0
Holcus lanatus	1.593	1.593	3	2	18.75	3.07	1.381	1.54	1.593	2.166	2.245	0.958	0.650	3.623	0
Hypericum perforatum	1.593	1.593	4	2	25.00	3.67	1.517	1.563	1.593	2.305	2.375	0.982	0.796	4.429	0

Impatiens parviflora	2.305	2.305	6	2	49.85	6.18	1.564	1.621	2.274	2.565	2.565	0.994	0.970	6.841	2
Lactuca muralis	2.166	2.011	4	2	16.18	1.6	0.404	0.553	2.011	2.226	2.305	0.862	0.474	2.214	0
Luzula pilosa	1.421	1.421	5	2	18.92	1.99	0.000	0.000	1.421	2.215	2.244	0.878	0.506	2.518	0
Lysimachia europaea	0.844	0.844	3	2	12.00	1.37	0.000	0.663	0.936	2.379	2.436	0.726	0.216	1.618	0
Melampyrum pratense	0.000	0.000	15	1	76.25	4.21	0.000	0.000	0.232	1.540	2.041	0.974	0.904	4.629	0
Pilosella officinarum	0.000	0.553	4	1	11.53	0.78	0.000	0.000	0.558	2.040	2.166	0.694	0.390	2.015	0
Pinus sylvestris	0.000	1.471	25	1	49.85	2.4	0.000	0.000	1.467	1.624	2.434	0.898	0.726	2.789	0
Poa nemoralis	2.166	2.166	3	2	18.04	2.44	0.303	0.315	2.059	2.196	2.245	0.848	0.468	2.508	0
Polygonatum odoratum	1.128	1.128	3	1	12.00	1.37	0.000	0.000	1.007	1.265	1.311	0.670	0.194	1.571	0
Prunus cerasifera	2.245	2.245	5	2	33.00	3.64	0.000	1.563	2.216	2.275	2.601	0.938	0.772	4.394	0
Prunus padus	0.553	0.553	3	2	10.34	0.75	0.000	0.404	1.471	1.817	1.866	0.670	0.224	1.463	0
Prunus serotina	0.000	0.083	43	2	95.84	7.3	0.000	0.000	0.315	0.844	0.885	1.000	1.000	7.200	2
Quercus petraea	2.565	1.563	43	1	68.15	1.73	0.000	0.000	1.478	2.305	2.565	0.924	0.782	2.642	0
Quercus robur	0.000	0.000	7	2	19.44	0.84	0.000	0.000	0.315	1.261	1.592	0.504	0.284	1.429	0
Quercus rubra	0.658	0.658	10	1	31.65	2.73	0.000	0.000	0.553	0.785	1.268	0.936	0.776	3.395	0
Robinia pseudoacacia	0.083	0.083	3	1	11.07	1.14	0.000	0.000	0.000	1.837	1.885	0.720	0.412	2.278	0
Rubus fruticosus agg	0.000	0.083	25	2	73.33	5.83	0.000	0.000	0.083	0.743	0.824	1.000	1.000	5.349	2
Rubus idaeus	2.215	2.215	12	2	51.92	4.53	0.743	0.762	1.593	2.215	2.244	1.000	0.990	5.236	2
Rumex acetosella	0.000	0.000	11	2	26.83	0.61	0.000	0.000	0.853	2.278	2.566	0.566	0.454	1.730	0
Sorbus aucuparia	0.000	0.000	34	2	74.04	3.21	0.000	0.000	0.232	1.695	2.166	0.970	0.902	3.666	0
Stellaria media	2.245	1.695	5	2	26.27	3.92	0.663	1.593	1.817	2.274	2.275	0.980	0.826	4.373	0
Vaccinium myrtillus	0.000	0.000	24	1	71.33	3.52	0.000	0.000	1.592	2.478	2.633	0.874	0.718	2.634	0
Vaccinium vitis idaea	0.315	0.315	6	1	19.16	1.76	0.000	0.000	0.315	1.563	2.215	0.818	0.574	2.383	0

Abbreviations: see **Table S6**.

Table S13. Results of Threshold Indicator Taxa Analysis for *P. serotina* in nutrient-rich sites in summer

Species	ienv.cp	zenv.cp	freq	maxgrp	IndVal	zscore	5%	10%	50%	90%	95%	purity	reliability	z.median	filter
Acer.platanoides	1.522	1.599	12	2	40.67	3.13	0.000	1.104	1.599	2.088	2.088	0.924	0.862	3.552	0
Acer.pseudoplatanus	0.000	1.135	25	2	40.10	0.79	0.000	0.087	1.458	2.718	2.826	0.562	0.506	1.998	0
Adoxa.moschatellina	0.000	0.000	3	1	12.97	1.48	0.000	0.000	0.000	2.2	2.2	0.668	0.384	2.761	0
Agrostis.capillaris	0.000	1.423	4	1	14.29	1.32	0.000	0.000	1.135	1.487	1.505	0.704	0.274	1.735	0
Alliaria.petiolata	2.718	2.718	13	2	49.34	3.06	0.000	0.000	2.279	2.892	3.11	0.694	0.636	2.792	0
Anemone.nemorosa	1.570	1.570	6	1	19.35	1.50	0.000	0.000	1.002	1.582	1.671	0.914	0.544	2.398	0
Avenella.flexuosa	0.000	0.364	6	1	18.80	1.52	0.000	0.000	0.364	1.835	1.86	0.864	0.416	2.014	0
Brachypodium.sylvaticum	1.944	1.944	24	1	46.76	1.06	0.000	0.000	0.706	1.944	1.954	0.550	0.348	1.524	0
Calamagrostis.arundinacea	1.701	0.472	6	2	22.22	2.77	0.364	0.405	1.329	1.944	2.243	0.976	0.778	3.295	0
Calamagrostis.epigejos	0.000	1.187	10	1	34.27	3.21	0.000	0.174	1.187	1.522	1.552	0.992	0.934	3.910	0
Carex.spicata	0.000	0.000	8	1	33.47	3.17	0.000	0.000	0.283	1.522	1.540	0.988	0.862	3.972	0
Carpinus.betulus	1.599	1.599	16	1	43.03	1.89	0.000	0.000	1.187	1.772	1.904	0.924	0.800	2.842	0
Chaerophyllum.temulum	0.000	0.000	8	1	35.79	4.13	0.000	0.000	0.000	0.993	1.599	0.906	0.800	3.668	0

Chelidonium.majus	2.718	1.072	8	2	24.85	2.13	0.000	0.754	1.517	3.001	3.110	0.924	0.770	3.341	0
Circaea.lutetiana	0.000	0.000	4	1	16.44	1.44	0.000	0.000	0.174	2.279	2.279	0.618	0.424	2.356	0
Convallaria.majalis	1.135	1.135	7	1	28.00	3.62	0.000	0.255	1.135	1.277	1.312	0.992	0.908	3.591	0
Corylus.avellana	2.088	2.088	3	2	21.51	3.70	0.000	0.000	2.072	2.823	3.001	0.842	0.600	3.545	0
Crataegus.monogyna	1.135	1.135	4	1	11.73	0.46	0.000	0.000	0.715	2.200	2.279	0.508	0.194	1.426	0
Crataegus.rhipidophylla	1.835	1.970	8	2	24.04	1.70	0.000	0.000	1.458	1.970	2.165	0.740	0.504	2.145	0
Dactylis.glomerata	0.364	0.364	17	2	34.79	1.18	0.000	0.000	1.522	3.001	3.110	0.746	0.606	2.248	0
Dryopteris.carthusiana	2.718	2.200	25	1	50.71	1.67	0.000	0.000	1.708	2.459	2.718	0.664	0.654	2.325	0
Dryopteris.filix.mas	1.072	1.072	15	2	30.22	0.84	0.000	0.000	0.765	1.599	1.920	0.688	0.424	1.722	0
Euonymus.europaeus	2.088	1.904	7	2	28.64	2.89	1.002	1.075	1.904	2.753	2.823	0.972	0.826	3.893	0
Fagus.sylvatica	1.002	1.002	20	1	42.85	0.90	0.000	0.000	1.002	2.279	2.718	0.612	0.492	1.868	0
Fallopia.convolvulus	2.279	0.000	32	2	55.90	1.60	0.000	0.000	0.465	2.279	2.459	0.888	0.762	2.825	0
Fragaria.vesca	1.522	1.522	3	1	10.00	0.72	0.000	0.000	0.706	1.522	1.552	0.526	0.112	1.338	0
Frangula.alnus	0.087	0.087	7	2	17.46	0.70	0.000	0.087	1.552	2.108	2.200	0.624	0.308	1.545	0
Fraxinus.excelsior	0.000	1.002	17	2	31.66	0.89	0.000	0.000	1.458	2.074	2.505	0.710	0.496	1.929	0
Galeopsis.tetrahit	1.835	1.835	35	1	57.56	0.99	0.000	0.000	0.000	1.835	1.961	0.526	0.374	1.482	0
Geranium.robertianum	1.002	1.002	25	2	59.53	2.46	0.087	0.364	1.002	2.088	2.204	0.952	0.864	3.348	0
Geum.urbanum	1.835	1.599	13	2	29.34	1.47	0.000	0.000	1.599	2.279	2.279	0.688	0.662	2.452	0
Hedera.helix	0.000	0.000	7	1	32.75	3.47	0.000	0.000	0.000	0.364	2.462	0.924	0.902	4.431	0
Hypericum.perforatum	0.174	1.423	6	1	21.43	1.93	0.000	0.000	0.255	1.458	1.487	0.950	0.660	2.637	0
Impatiens.parviflora	2.718	1.996	37	2	63.65	2.03	0.000	0.000	1.996	2.279	2.718	0.730	0.776	2.621	0
Juncus.effusus	1.522	1.522	6	1	20.00	1.85	0.000	0.174	1.487	1.570	1.599	0.816	0.420	1.958	0
Lactuca.muralis	0.000	0.000	25	1	45.26	1.21	0.000	0.000	1.135	2.460	2.823	0.726	0.534	2.079	0
Lamium.galeobdolon	1.570	1.599	6	1	15.48	0.71	0.000	0.000	1.062	1.587	1.929	0.702	0.302	1.644	0
Lolium.giganteum	0.087	1.002	5	2	15.41	1.14	0.087	0.087	1.072	2.503	2.823	0.808	0.364	1.804	0
Luzula.pilosa	0.000	1.835	8	1	23.53	1.56	0.000	0.000	0.283	1.835	1.875	0.884	0.542	2.277	0
Maianthemum.bifolium	2.279	2.279	9	1	21.95	0.28	0.087	0.376	1.671	2.236	2.236	0.376	0.206	-1.746	0
Melampyrum.pratense	0.000	0.000	5	1	19.00	1.78	0.000	0.000	0.310	1.701	2.089	0.646	0.344	1.825	0
Melica.uniflora	1.423	1.423	4	1	14.29	1.21	0.282	0.364	0.768	1.458	1.458	0.680	0.280	1.632	0
Milium.effusum	1.570	1.570	6	1	15.58	0.83	0.000	0.000	1.062	1.859	2.322	0.572	0.266	1.654	0
Moehringia.trinervia	2.718	1.458	27	2	55.54	2.48	0.000	0.000	1.996	2.892	3.001	0.950	0.818	3.305	0
Oxalis.acetosella	0.000	0.000	8	1	45.26	4.74	0.000	0.000	1.002	1.075	1.135	0.998	0.966	4.411	1
Pinus.sylvestris	0.000	0.000	3	1	32.18	4.50	0.000	0.000	0.000	0.707	0.775	0.942	0.462	2.771	0
Poa.nemoralis	2.503	0.000	31	2	49.14	0.90	0.000	0.000	1.211	2.503	3.001	0.502	0.672	2.340	0
Polygonatum.odoratum	1.944	1.904	3	2	23.08	4.46	1.701	1.835	1.944	2.200	2.755	0.968	0.762	5.179	0
Prunus.avium	0.000	0.000	5	1	26.40	2.85	0.000	0.000	0.000	2.200	2.823	0.686	0.618	3.298	0
Prunus.cerasifera	1.970	1.970	11	2	35.52	2.52	0.000	0.000	1.954	2.088	2.098	0.894	0.700	3.134	0
Prunus.padus	1.970	1.970	11	2	53.11	5.05	1.329	1.716	1.957	2.088	2.098	0.990	0.962	5.241	2
Prunus.serotina	0.087	0.405	34	2	85.74	6.56	0.000	0.087	0.458	1.588	1.689	1.000	1.000	6.658	2
Pteridium.aquilinum	0.000	0.759	10	1	40.49	4.41	0.000	0.364	0.759	1.017	1.131	1.000	0.984	4.616	1
Pyrus.communis	1.944	1.944	9	2	23.53	1.49	0.000	0.000	1.329	1.954	2.200	0.836	0.512	2.324	0
Quercus.petraea	1.701	1.522	34	1	75.98	3.19	0.364	0.472	1.329	1.701	1.745	0.998	0.974	3.679	1
Quercus.robur	2.718	2.718	7	2	76.34	7.15	1.002	1.781	2.538	2.897	3.001	0.976	0.912	7.533	0

Quercus.rubra	2.088	2.088	5	1	12.82	0.35	0.000	0.000	0.759	1.554	1.955	0.566	0.286	1.461	0
Ribes.rubrum	1.002	1.002	3	2	12.00	1.41	0.295	0.715	1.197	1.745	1.835	0.736	0.268	1.694	0
Ribes.uva.crispa	0.405	0.405	5	2	17.86	1.96	0.296	0.364	0.83	1.745	1.835	0.894	0.452	2.325	0
Robinia.pseudoacacia	1.423	1.423	4	1	14.29	1.62	0.000	0.000	1.072	1.487	1.505	0.638	0.302	1.864	0
Rubus.caesius	0.000	0.000	10	2	23.81	0.44	0.000	0.000	1.002	1.970	2.171	0.550	0.530	2.258	0
Rubus.fruticosus.agg.	2.503	2.503	25	1	51.51	0.93	0.000	0.000	1.552	2.279	2.503	0.532	0.500	1.889	0
Rubus.idaeus	2.279	1.970	17	1	39.19	1.39	0.000	0.000	1.329	1.970	2.243	0.832	0.552	2.005	0
Sambucus.nigra	1.423	1.423	15	2	31.24	0.99	0.000	0.472	1.522	1.920	2.166	0.654	0.468	1.879	0
Scrophularia.nodosa	1.599	1.599	3	2	11.54	1.29	0.000	0.000	1.582	2.247	2.279	0.702	0.318	1.971	0
Sorbus.aucuparia	2.503	0.000	17	2	39.11	1.65	0.000	0.000	1.073	2.503	2.503	0.660	0.614	2.193	0

Abbreviations: see **Table S6**.

Table S14. The parameters of Generalized Linear Mixed-Effect Models for the impact of *R. pseudoacacia* aboveground biomass (AB) on different plant diversity indicators on nutrient-poor sites in spring. Abbreviation in parentheses for each species indicates the distribution of dependent variable.

Response	Variable	Estimate	SE	z	Pr(>|z|)
rich (NB)	(Intercept)	2.3539	0.2353	10.006	< 0.001
obs. = 48	Age	0.0062	0.0026	2.4320	0.015
AICc = 334.1					
$AICc_0$ = 338.6					
Random effect SD:					
Year = 0.1979					
Forest District < 0.0001					
shan (G)	(Intercept)	0.6698	0.3343	2.004	0.0451
obs. = 48	Age	0.0102	0.0038	2.659	0.0078
AICc = 100.2					
$AICc_0$ = 105.8					
Random effect SD:					
Year = 0.2348					
Forest District < 0.0001					
FRic (G)	(Intercept)	0.0894	0.0920	0.971	0.3310
obs. = 47					
AICc = 98.1					
$AICc_0$ = 99					
Random effect SD:					
Year < 0.0001					

Forest District < 0.0001					
FDis (G)	(Intercept)	-0.5349	0.1590	-3.364	0.0008
obs. = 47	log1p(Biomass)	0.1985	0.0719	2.759	0.0058
AICc = 113.5					
$AICc_0$ = 119.5					
Random effect SD:					
Year < 0.0001					
Forest District < 0.0001					
PD (G)	(Intercept)	0.0340	0.1013	0.335	0.7380
obs. = 48					
AICc = 110.2					
$AICc_0$ = 111.2					
Random effect SD:					
Year < 0.0001					
Forest District < 0.0001					
MPD (G)	(Intercept)	0.2557	0.1206	2.120	0.0340
obs. = 48	log1p(Biomass)	-0.1346	0.0551	-2.442	0.0146
AICc = 91.4					
$AICc_0$ = 95.9					
Random effect SD:					
Year < 0.0001					
Forest District < 0.0001					
EIV.L (G)	(Intercept)	5.7909	0.1122	51.610	< 0.001
obs. = 48					
AICc = 120					
$AICc_0$ = 121					
Random effect SD:					
Year < 0.0001					
Forest District < 0.0001					
EIV.M (G)	(Intercept)	4.9077	0.0843	58.220	< 0.001
obs. = 48	log1p(Biomass)	0.1190	0.0385	3.090	0.0020
AICc = 57					
$AICc_0$ = 64.6					
Random effect SD:					
Year < 0.0001					
Forest District < 0.0001					
EIV.N (G)	(Intercept)	3.8682	0.2484	15.570	< 0.001
obs. = 48	log1p(Biomass)	0.5610	0.1136	4.939	< 0.001
AICc = 160.8					

$AICc_0$ = 178.7					
Random effect SD:					
Year < 0.0001					
Forest District < 0.0001					
EIV.SR (G)	(Intercept)	3.8777	0.6238	6.217	< 0.001
obs. = 48	log1p(Biomass)	0.6946	0.1268	5.479	< 0.001
AICc = 165.8	Age	-0.0082	0.0079	-1.048	0.2940
$AICc_0$ = 187.5					
Random effect SD:					
Year = 0.1130					
Forest District = 0.0002					
SLA (G)	(Intercept)	218.7849	48.7729	4.486	< 0.001
obs. = 48	log1p(Biomass)	24.6996	9.3739	2.635	0.0084
AICc = 582.8	Age	-0.1687	0.6161	-0.274	0.7842
$AICc_0$ = 585.7					
Random effect SD:					
Year = 0.0076					
Forest District <0.001					
H (G)	(Intercept)	0.3235	0.0981	3.299	0.0010
obs. = 48	log1p(Biomass)	0.0728	0.0342	2.131	0.0331
AICc = 45.2					
$AICc_0$ = 48.4					
Random effect SD:					
Year < 0.0001					
Forest District = 0.1131					
SM (G)	(Intercept)	1.6874	0.3580	4.713	< 0.001
obs. = 48	Age	-0.0070	0.0043	-1.633	0.1030
AICc = 110.2					
$AICc_0$ = 111.7					
Random effect SD:					
Year < 0.0001					
Forest District = 0.2441					

Abbreviations: **SE** – standard error; **z** – z-test statistic; **Pr(>|z|)** – p-value; **AICc** – Akaike's Information Criterion; **$AICc_0$** – AICc of null model; **SD** – standard deviation; **NB** – negative binomial distribution; **G ─** Gaussian distribution; **FRic ─** SES Functional richness; **FDis ─** SES Functional dispersion; **PD ─** Faith's phylogenetic diversity; **MPD ─** Mean Pairwise Distance; **rich ─** Species richness; **shan ─** Shannon's diversity index; **EIV.L ─** Light Ecological Indicator Value; **EIV.M ─** Moisture Ecological Indicator Value; **EIV.N ─** Soil Fertility Ecological Indicator Value; **EIV.SR ─** Soil Reaction Ecological Indicator Value; **SLA ─** Specific Leaf Area CWM [$cm^2\ g^{-1}$]; **H ─** Maximum height CWM [m]; **SM ─** Seed mass CWM [mg]

Table S15. The parameters of Generalized Linear Mixed-Effect Models for the impact of *R. pseudoacacia* aboveground biomass (AB) on different plant diversity indicators on nutrient-rich sites in spring. Abbreviation in parentheses for each species indicates the distribution of dependent variable.

Response	Variable	Estimate	SE	Z	Pr(>|z|)
rich (NB)	(Intercept)	3.0945	0.0555	55.800	< 0.001
obs. = 48					
AICc = 332.9					
$AICc_0$ = 333.9					
Random effect SD:					
Year < 0.0001					
Forest District = 0.0599					
shan (G)	(Intercept)	1.7911	0.1011	17.720	< 0.001
obs. = 48					
AICc = 74.3					
$AICc_0$ = 75.2					
Random effect SD:					
Year < 0.0001					
Forest District = 0.1650					
FRic (G)	(Intercept)	-0.3646	0.1112	-3.279	0.0010
obs. = 48					
AICc = 119.2					
$AICc_0$ = 120.1					
Random effect SD:					
Year < 0.0001					
Forest District < 0.0001					
FDis (G)	(Intercept)	-0.2101	0.1366	-1.539	0.1240
obs. = 48	log1p(Biomass)	-0.0866	0.0500	-1.734	0.0830
AICc = 104.9					
$AICc_0$ = 106.6					
Random effect SD:					
Year < 0.0001					
Forest District < 0.0001					
PD (G)	(Intercept)	-0.5212	0.2026	-2.572	0.0101
obs. = 48	log1p(Biomass)	0.1121	0.0572	1.961	0.0499

AICc = 116.8					
$AICc_0$ = 119.4					
Random effect SD:					
Year = 0.2245					
Forest District < 0.0001					
MPD (G)	log1p(Biomass)	0.1386	0.0567	2.445	0.0145
obs. = 48	Age	-0.0077	0.0034	-2.261	0.0237
AICc = 119.9					
$AICc_0$ = 125.1					
Random effect SD:					
Year < 0.0001					
Forest District = 0.3787					
EIV.L (G)	(Intercept)	4.9177	0.0974	50.500	< 0.001
obs. = 48	log1p(Biomass)	-0.0623	0.0356	-1.750	0.0803
AICc = 72.5					
$AICc_0$ = 74.4					
Random effect SD:					
Year < 0.0001					
Forest District < 0.0001					
EIV.M (G)	(Intercept)	5.2829	0.0886	59.660	< 0.001
obs. = 48					
AICc = 31.9					
$AICc_0$ = 32.9					
Random effect SD:					
Year < 0.0001					
Forest District = 0.1728					
EIV.N (G)	(Intercept)	5.0389	0.4176	12.060	< 0.001
obs. = 48	Age	0.0078	0.0041	1.910	0.0561
AICc = 139.2					
$AICc_0$ = 141.6					
Random effect SD:					
Year = 0.1871					
Forest District < 0.0001					
EIV.SR (G)	(Intercept)	5.3027	0.3561	14.890	< 0.001
obs. = 48	Age	0.0065	0.0033	1.968	0.0491
AICc = 119.8					
$AICc_0$ = 122.5					
Random effect SD:					
Year = 0.2461					

Forest District < 0.0001					
SLA (G)	(Intercept)	425.8500	31.4700	13.530	< 0.001
obs. = 48					
AICc = 616.9					
$AICc_0$ = 617.4					
Random effect SD:					
Year = 41.6700					
Forest District < 0.0001					
H (G)	(Intercept)	0.4648	0.0759	6.125	< 0.001
obs. = 48					
AICc = 47					
$AICc_0$ = 47.9					
Random effect SD:					
Year = 0.0957					
Forest District < 0.0001					
SM (G)	(Intercept)	1.3431	0.1019	13.186	< 0.001
obs. = 48	log1p(Biomass)	-0.0509	0.0317	-1.606	0.1080
AICc = 57.8					
$AICc_0$ = 59.3					
Random effect SD:					
Year = 0.0971					
Forest District < 0.0001					

Abbreviations: **SE** – standard error; **z** – z-test statistic; **Pr(>|z|)** – p-value; **AICc** – Akaike's Information Criterion; **$AICc_0$** – AICc of null model; **SD** – standard deviation; **NB** – negative binomial distribution; **G** ─ Gaussian distribution; **FRic** ─ SES Functional richness; **FDis** ─ SES Functional dispersion; **PD** ─ Faith's phylogenetic diversity; **MPD** ─ Mean Pairwise Distance; **rich** ─ Species richness; **shan** ─ Shannon's diversity index; **EIV.L** ─ Light Ecological Indicator Value; **EIV.M** ─ Moisture Ecological Indicator Value; **EIV.N** ─ Soil Fertility Ecological Indicator Value; **EIV.SR** ─ Soil Reaction Ecological Indicator Value; **SLA** ─ Specific Leaf Area CWM [$cm^2\ g^{-1}$]; **H** ─ Maximum height CWM [m]; **SM** ─ Seed mass CWM [mg]

Table S16. The parameters of Generalized Linear Mixed-Effect Models for the impact of *P. serotina* aboveground biomass (AB) on different plant diversity indicators on nutrient-poor sites in spring. Abbreviation in parentheses for each species indicates the distribution of dependent variable.

Response	Variable	Estimate	SE	z	Pr(>|z|)
rich (P)	(Intercept)	2.2569	0.1394	16.185	< 0.001
obs. = 47	log1p(Biomass)	0.1273	0.0462	2.758	0.0058
AICc = 270.6					
$AICc_0$ = 276.8					
Random effect SD:					
Year = 0.1708					
Forest District = 0.0919					
shan (G)	(Intercept)	1.3954	0.3242	4.304	< 0.001
obs. = 47	log1p(Biomass)	0.1742	0.0754	2.309	0.0210
AICc = 82.5	Age	-0.0076	0.0034	-2.204	0.0275
$AICc_0$ = 89.4					
Random effect SD:					
Year = 0.3007					
Forest District < 0.0001					
FRic (G)	(Intercept)	0.1778	0.2266	0.785	0.4330
obs. = 46					
AICc = 88					
$AICc_0$ = 88.9					
Random effect SD:					
Year = 0.0004					
Forest District = 0.4170					
FDis (G)	(Intercept)	-0.5998	0.1716	-3.496	0.0005
obs. = 46	log1p(Biomass)	0.2369	0.1130	2.096	0.0360
AICc = 117.1					
$AICc_0$ = 120.3					
Random effect SD:					
Year < 0.0001					
Forest District < 0.0001					
PD (G)	(Intercept)	0.1047	0.0939	1.115	0.2650
obs. = 47					
AICc = 100					
$AICc_0$ = 100.9					
Random effect SD:					
Year < 0.0001					
Forest District < 0.0001					
MPD (G)	(Intercept)	0.3922	0.0728	5.388	< 0.001
obs. = 47					
AICc = 76					

$AICc_0$ = 77					
Random effect SD:					
Year < 0.0001					
Forest District < 0.0001					
EIV.L (G)	(Intercept)	5.8746	0.1084	54.180	< 0.001
obs. = 47					
AICc = 113.5					
$AICc_0$ = 114.5					
Random effect SD:					
Year < 0.0001					
Forest District < 0.0001					
EIV.M (G)	(Intercept)	4.8972	0.0562	87.170	< 0.001
obs. = 47					
AICc = 51.7					
$AICc_0$ = 52.6					
Random effect SD:					
Year < 0.0001					
Forest District < 0.0001					
EIV.N (G)	(Intercept)	3.5864	0.2081	17.232	< 0.001
obs. = 47	log1p(Biomass)	0.3329	0.1385	2.403	0.0162
AICc = 139.9					
$AICc_0$ = 144.3					
Random effect SD:					
Year < 0.0001					
Forest District < 0.0001					
EIV.SR (G)	(Intercept)	2.9414	0.2657	11.069	< 0.001
obs. = 47	log1p(Biomass)	0.6942	0.1769	3.925	< 0.001
AICc = 162.8					
$AICc_0$ = 173.8					
Random effect SD:					
Year < 0.0001					
Forest District < 0.0001					
SLA (G)	(Intercept)	197.2010	10.0390	19.643	< 0.001
obs. = 47	log1p(Biomass)	15.3160	6.6820	2.292	0.0219
AICc = 504.2					
$AICc_0$ = 508.1					
Random effect SD:					
Year = 0.0054					
Forest District = 0.0371					

H (G)	(Intercept)	0.3635	0.0738	4.923	< 0.001
obs. = 47	log1p(Biomass)	0.2574	0.0491	5.238	< 0.001
AICc = 42.4					
$AICc_0$ = 60.4					
Random effect SD:					
Year < 0.0001					
Forest District < 0.0001					
SM (G)	(Intercept)	2.1622	0.3202	6.753	< 0.001
obs. = 47	Age	-0.0103	0.0042	-2.422	0.0154
AICc = 98.8					
$AICc_0$ = 103.2					
Random effect SD:					
Year < 0.0001					
Forest District < 0.0001					

Abbreviations: **SE** – standard error; **z** – z-test statistic; **Pr(>|z|)** – p-value; **AICc** – Akaike's Information Criterion; **$AICc_0$** – AICc of null model; **SD** – standard deviation; **P** – Poisson distribution; **G ─** Gaussian distribution; **FRic ─** SES Functional richness; **FDis ─** SES Functional dispersion; **PD ─** Faith's phylogenetic diversity; **MPD ─** Mean Pairwise Distance; **rich ─** Species richness; **shan ─** Shannon's diversity index; **EIV.L ─** Light Ecological Indicator Value; **EIV.M ─** Moisture Ecological Indicator Value; **EIV.N ─** Soil Fertility Ecological Indicator Value; **EIV.SR ─** Soil Reaction Ecological Indicator Value; **SLA ─** Specific Leaf Area CWM [$cm^2\ g^{-1}$]; **H ─** Maximum height CWM [m]; **SM ─** Seed mass CWM [mg]

Table S17. The parameters of Generalized Linear Mixed-Effect Models for the impact of *P. serotina* aboveground biomass (AB) on different plant diversity indicators on nutrient-rich sites in spring. Abbreviation in parentheses for each species indicates the distribution of dependent variable.

Response	Variable	Estimate	SE	z	Pr(>|z|)
rich (NB)	(Intercept)	3.1218	0.0443	70.520	< 0.001
obs. = 48					
AICc = 328.2					
$AICc_0$ = 329.2					
Random effect SD:					
Year < 0.0001					

Forest District < 0.0001					
shan (G)	(Intercept)	1.8491	0.0995	18.580	< 0.001
obs. = 48					
AICc = 64.8					
$AICc_0$ = 65.7					
Random effect SD:					
Year = 0.1268					
Forest District < 0.0001					
FRic (G)	(Intercept)	-0.3302	0.1083	-3.049	0.0023
obs. = 48					
AICc = 116.6					
$AICc_0$ = 117.6					
Random effect SD:					
Year < 0.0001					
Forest District < 0.0001					
FDis (G)	(Intercept)	-0.1728	0.1011	-1.709	0.0875
obs. = 48					
AICc = 110.1					
$AICc_0$ = 111					
Random effect SD:					
Year < 0.0001					
Forest District < 0.0001					
PD (G)	(Intercept)	-0.7636	0.3289	-2.322	0.0203
obs. = 48	Age	0.0051	0.0032	1.579	0.1144
AICc = 106.2					
$AICc_0$ = 107.7					
Random effect SD:					
Year = 0.0781					
Forest District = 0.0005					
MPD (G)	(Intercept)	-0.3799	0.2337	-1.625	0.1040
obs. = 48					
AICc = 115.4					
$AICc_0$ = 116.3					
Random effect SD:					
Year = 0.0001					
Forest District = 0.4162					
EIV.L (G)	(Intercept)	4.8994	0.0720	68.020	< 0.001
obs. = 48					
AICc = 77.5					

$AICc_0$ = 78.4					
Random effect SD:					
Year < 0.0001					
Forest District < 0.0001					
EIV.M (G)	(Intercept)	5.1929	0.0958	54.220	< 0.001
obs. = 48					
AICc = 22.4					
$AICc_0$ = 23.3					
Random effect SD:					
Year < 0.0001					
Forest District = 0.1838					
EIV.N (G)	(Intercept)	4.6584	0.4012	11.612	< 0.001
obs. = 48	log1p(Biomass)	0.2065	0.1228	1.681	0.0928
AICc = 133.4	Age	0.0067	0.0042	1.609	0.1076
$AICc_0$ = 136					
Random effect SD:					
Year < 0.0001					
Forest District = 0.1165					
EIV.SR (G)	log1p(Biomass)	0.2592	0.1160	2.234	0.0255
obs. = 48	Age	0.0082	0.0039	2.106	0.0352
AICc = 125.6					
$AICc_0$ = 130.9					
Random effect SD:					
Year < 0.0001					
Forest District = 0.2475					
SLA (G)	(Intercept)	191.6286	56.1944	3.410	0.0006
obs. = 48	log1p(Biomass)	49.8322	16.8524	2.957	0.0031
AICc = 608.2	Age	1.8641	0.5677	3.284	0.0010
$AICc_0$ = 610.9					
Random effect SD:					
Year = 2.9060					
Forest District = 123.0280					
H (G)	(Intercept)	0.4451	0.0716	6.218	< 0.001
obs. = 48	log1p(Biomass)	0.11491	0.0467	2.460	0.0139
AICc = 43.8					
$AICc_0$ = 48.5					
Random effect SD:					
Year < 0.0001					
Forest District < 0.0001					

SM (G)	(Intercept)	1.4102	0.0650	21.690	< 0.001
obs. = 48					
AICc = 67.7					
$AICc_0$ = 68.6					
Random effect SD:					
Year < 0.0001					
Forest District < 0.0001					

Abbreviations: **SE** – standard error; **z** – z-test statistic; **Pr(>|z|)** – p-value; **AICc** – Akaike's Information Criterion; **$AICc_0$** – AICc of null model; **SD** – standard deviation; **NB** – negative binomial distribution; **G ─** Gaussian distribution; **FRic ─** SES Functional richness; **FDis ─** SES Functional dispersion; **PD ─** Faith's phylogenetic diversity; **MPD ─** Mean Pairwise Distance; **rich ─** Species richness; **shan ─** Shannon's diversity index; **EIV.L ─** Light Ecological Indicator Value; **EIV.M ─** Moisture Ecological Indicator Value; **EIV.N ─** Soil Fertility Ecological Indicator Value; **EIV.SR ─** Soil Reaction Ecological Indicator Value; **SLA ─** Specific Leaf Area CWM [$cm^2\ g^{-1}$]; **H ─** Maximum height CWM [m]; **SM ─** Seed mass CWM [mg]

Table S18. The parameters of Generalized Linear Mixed-Effect Models for the impact of *R. pseudoacacia* aboveground biomass (AB) on different plant diversity indicators on nutrient-poor sites in summer. Abbreviation in parentheses for each species indicates the distribution of dependent variable.

Response	Variable	Estimate	SE	z	Pr(>|z|)
rich (P)	(Intercept)	2.7157	0.1821	14.91	< 0.001
obs. = 48	log1p(Biomass)	0.1388	0.0273	5.08	< 0.001
AICc = 283.4	Age	-0.0042	0.0019	-2.256	0.0241
$AICc_0$ = 306.9					
Random effect SD:					
Year = 0.1950					
Forest District < 0.0001					
shan (G)	(Intercept)	1.4061	0.2597	5.414	< 0.001
obs. = 48	log1p(Biomass)	0.1945	0.0483	4.024	< 0.001
AICc = 79.6	Age	-0.0056	0.0031	-1.788	0.0738
$AICc_0$ = 91.3					
Random effect SD:					
Year = 0.1404					
Forest District < 0.0001					
FRic (G)	(Intercept)	-0.0476	0.0948	-0.503	0.6150

obs. = 48					
AICc = 103.8					
$AICc_0$ = 104.7					
Random effect SD:					
Year < 0.0001					
Forest District < 0.0001					
FDis (G)	(Intercept)	-0.2647	0.1150	-2.301	0.0214
obs. = 48					
AICc = 122.4					
$AICc_0$ = 123.4					
Random effect SD:					
Year < 0.0001					
Forest District < 0.0001					
PD (G)	(Intercept)	0.0026	0.1155	0.022	0.9820
obs. = 48					
AICc = 122.8					
$AICc_0$ = 123.8					
Random effect SD:					
Year < 0.0001					
Forest District < 0.0001					
MPD (G)	(Intercept)	0.2065	0.1552	1.331	0.1833
obs. = 48	log1p(Biomass)	-0.1174	0.0709	-1.655	0.0979
AICc = 115.6					
$AICc_0$ = 117.2					
Random effect SD:					
Year < 0.0001					
Forest District < 0.0001					
EIV.L (G)	(Intercept)	6.5348	0.3649	17.909	< 0.001
obs. = 48	Age	-0.0091	0.0045	-2.028	0.0426
AICc = 112.4					
$AICc_0$ = 115.2					
Random effect SD:					
Year = 0.00001701					
Forest District = 0.0967					
EIV.M (G)	(Intercept)	4.7608	0.0712	66.850	< 0.001
obs. = 48	log1p(Biomass)	0.1356	0.0326	4.160	< 0.001
AICc = 38.8					
$AICc_0$ = 52.2					
Random effect SD:					

Year < 0.0001					
Forest District < 0.0001					
EIV.N (G)	(Intercept)	3.6506	0.20552	17.762	< 0.001
obs. = 48	log1p(Biomass)	0.6112	0.09396	6.505	< 0.001
AICc = 142.6					
$AICc_0$ = 171.3					
Random effect SD:					
Year < 0.0001					
Forest District < 0.0001					
EIV.SR (G)	(Intercept)	3.1703	0.2586	12.259	< 0.001
obs. = 48	log1p(Biomass)	0.7434	0.1182	6.288	< 0.001
AICc = 164.6					
$AICc_0$ = 191.4					
Random effect SD:					
Year < 0.0001					
Forest District < 0.0001					
SLA (G)	(Intercept)	202.6300	29.5900	6.849	< 0.001
obs. = 48	log1p(Biomass)	35.7600	10.7000	3.343	0.0008
AICc = 597.1					
$AICc_0$ = 606.1					
Random effect SD:					
Year = 21.4690					
Forest District = 0.0011					
H (G)	(Intercept)	0.5011	0.0581	8.628	< 0.001
obs. = 48					
AICc = 37.7					
$AICc_0$ = 38.6					
Random effect SD:					
Year < 0.0001					
Forest District = 0.0319					
SM (G)	(Intercept)	1.5056	0.1779	8.466	< 0.001
obs. = 48	log1p(Biomass)	-0.0949	0.0573	-1.655	0.0979
AICc = 94.5					
$AICc_0$ = 96.1					
Random effect SD:					
Year = 0.2081					
Forest District < 0.0001					

Abbreviations: **SE** – standard error; **z** – z-test statistic; **Pr(>|z|)** – p-value; **AICc** – Akaike's Information Criterion; **$AICc_0$** – AICc of null model; **SD** – standard deviation; **P** – Poisson distribution; **G ─** Gaussian distribution; **FRic ─** SES Functional richness; **FDis ─** SES Functional dispersion; **PD ─** Faith's phylogenetic diversity; **MPD ─** Mean Pairwise Distance; **rich ─** Species richness; **shan ─** Shannon's diversity index; **EIV.L ─** Light Ecological Indicator Value; **EIV.M ─** Moisture Ecological Indicator Value; **EIV.N ─** Soil Fertility Ecological Indicator Value; **EIV.SR ─** Soil Reaction Ecological Indicator Value; **SLA ─** Specific Leaf Area CWM [$cm^2\ g^{-1}$]; **H ─** Maximum height CWM [m]; **SM ─** Seed mass CWM [mg]

Table S19. The parameters of Generalized Linear Mixed-Effect Models for the impact of *R. pseudoacacia* aboveground biomass (AB) on different plant diversity indicators on nutrient-rich sites in summer. Abbreviation in parentheses for each species indicates the distribution of dependent variable.

Response	Variable	Estimate	SE	z	Pr(>|z|)
rich (NB) obs. = 48 AICc = 321 $AICc_0$ = 321.9 Random effect SD: Year = 0.0991 Forest District = 0.0318	(Intercept)	2.9974	0.0753	39.79	< 0.001
shan (G) obs. = 48 AICc = 78.2 $AICc_0$ = 79.1 Random effect SD: Year = 0.1300 Forest District = 0.1224	(Intercept)	1.7318	0.1189	14.560	< 0.001
FRic (G) obs. = 48 AICc = 119.4 $AICc_0$ = 120.4 Random effect SD: Year = 0.1294	(Intercept)	-0.6304	0.1394	-4.523	< 0.001

Forest District < 0.0001					
FDis (G)	(Intercept)	-0.3244	0.1334	-2.432	0.015
obs. = 48	log1p(Biomass)	-0.1245	0.0488	-2.551	0.0107
AICc = 102.7					
$AICc_0$ = 107.7					
Random effect SD:					
Year < 0.0001					
Forest District < 0.0001					
PD (G)	(Intercept)	0.0655	0.3631	0.180	0.8568
obs. = 48	log1p(Biomass)	0.1284	0.0586	2.191	0.0284
AICc = 117.2	Age	-0.0045	0.0035	-1.281	0.2001
$AICc_0$ = 119					
Random effect SD:					
Year = 0.1760					
Forest District = 0.1498					
MPD (G)	(Intercept)	0.5007	0.3895	1.286	0.1986
obs. = 48	log1p(Biomass)	0.1136	0.0581	1.956	0.0505
AICc = 122.7	Age	-0.0100	0.0034	-2.947	0.0032
$AICc_0$ = 128.9					
Random effect SD:					
Year < 0.0001					
Forest District = 0.4245					
EIV.L (G)	(Intercept)	4.9841	0.1536	32.450	< 0.001
obs. = 48	log1p(Biomass)	-0.0812	0.0457	-1.780	0.0758
AICc = 96.3					
$AICc_0$ = 98.3					
Random effect SD:					
Year = 0.1532					
Forest District < 0.0001					
EIV.M (G)	(Intercept)	5.1729	0.0586	88.390	< 0.001
obs. = 48					
AICc = 18.6					
$AICc_0$ = 19.6					
Random effect SD:					
Year = 0.0743					
Forest District < 0.0001					
EIV.N (G)	(Intercept)	5.8618	0.1165	50.330	< 0.001
obs. = 48					
AICc = 123.6					

$AICc_0$ = 124.6					
Random effect SD:					
Year < 0.0001					
Forest District < 0.0001					
EIV.SR (G)	(Intercept)	5.4537	0.3621	15.06	< 0.001
obs. = 48	Age	0.0065	0.0036	1.790	0.0734
AICc = 128.8					
$AICc_0$ = 130.8					
Random effect SD:					
Year < 0.0001					
Forest District < 0.0001					
SLA (G)	(Intercept)	347.0735	76.2498	4.552	< 0.001
obs. = 48	Age	1.2484	0.7627	1.637	0.1020
AICc = 642.3					
$AICc_0$ = 643.9					
Random effect SD:					
Year = 0.0080					
Forest District < 0.0001					
H (G)	(Intercept)	0.5988	0.0555	10.780	< 0.001
obs. = 48					
AICc = 34.9					
$AICc_0$ = 35.8					
Random effect SD:					
Year = 0.0468					
Forest District < 0.0001					
SM (G)	(Intercept)	1.4230	0.0719	19.780	< 0.001
obs. = 48					
AICc = 55.1					
$AICc_0$ = 56					
Random effect SD:					
Year < 0.0001					
Forest District = 0.0929					

Abbreviations: **SE** – standard error; **z** – z-test statistic; **Pr(>|z|)** – p-value; **AICc** – Akaike's Information Criterion; **$AICc_0$** – AICc of null model; **SD** – standard deviation; **NB** – negative binomial distribution; **G ─** Gaussian distribution; **FRic ─** SES Functional richness; **FDis ─** SES Functional dispersion; **PD ─** Faith's phylogenetic diversity; **MPD ─** Mean Pairwise Distance; **rich ─** Species richness; **shan ─** Shannon's diversity index; **EIV.L ─** Light Ecological Indicator Value; **EIV.M ─** Moisture Ecological Indicator Value; **EIV.N ─** Soil Fertility Ecological Indicator Value; **EIV.SR ─** Soil Reaction Ecological Indicator Value; **SLA ─** Specific Leaf Area CWM [$cm^2\ g^{-1}$]; **H ─** Maximum height CWM [m]; **SM ─** Seed mass CWM [mg]

Table S20. The parameters of Generalized Linear Mixed-Effect Models for the impact of *P. serotina* aboveground biomass (AB) on different plant diversity indicators on nutrient-poor sites in summer. Abbreviation in parentheses for each species indicates the distribution of dependent variable.

Response	Variable	Estimate	SE	z	Pr(>|z|)
rich (P)	(Intercept)	2.6995	0.2262	11.932	< 0.001
obs. = 47	log1p(Biomass)	0.1220	0.0460	2.653	0.0080
AICc = 264.8	Age	-0.0068	0.0021	-3.275	0.0011
$AICc_0$ = 280.2					
Random effect SD:					
Year = 0.2703					
Forest District < 0.0001					
shan (G)	(Intercept)	1.5524	0.3357	4.624	< 0.001
obs. = 47	log1p(Biomass)	0.1475	0.0767	1.921	0.0547
AICc = 84.4	Age	-0.0088	0.0035	-2.532	0.0114
$AICc_0$ = 91.1					
Random effect SD:					
Year = 0.3254					
Forest District < 0.0001					
FRic (G)	(Intercept)	-0.0173	0.2079	-0.083	0.9336
obs. = 47	log1p(Biomass)	0.2673	0.0825	3.239	0.0012
AICc = 88					
$AICc_0$ = 96.6					
Random effect SD:					
Year = 0.2055					
Forest District = 0.1689					
FDis (G)	(Intercept)	-0.5575	0.1855	-3.006	0.0027
obs. = 47	log1p(Biomass)	0.2261	0.1163	1.943	0.0520
AICc = 114.7					
$AICc_0$ = 117.4					
Random effect SD:					
Year = 0.1265					
Forest District < 0.0001					

PD (G)	(Intercept)	0.0073	0.1144	0.064	0.9490
obs. = 47					
AICc = 118.5					
$AICc_0$ = 119.5					
Random effect SD:					
Year < 0.0001					
Forest District < 0.0001					
MPD (G)	(Intercept)	0.2511	0.0935	2.687	0.0072
obs. = 47					
AICc = 99.5					
$AICc_0$ = 100.5					
Random effect SD:					
Year < 0.0001					
Forest District < 0.0001					
EIV.L (G)	(Intercept)	6.3602	0.3171	20.056	< 0.001
obs. = 47	Age	-0.0072	0.0040	-1.819	0.0689
AICc = 93.9					
$AICc_0$ = 96					
Random effect SD:					
Year = 0.1966					
Forest District < 0.0001					
EIV.M (G)	(Intercept)	4.6939	0.0563	83.40	< 0.001
obs. = 47	log1p(Biomass)	0.0892	0.0375	2.380	0.0173
AICc = 16.9					
$AICc_0$ = 21.2					
Random effect SD:					
Year < 0.0001					
Forest District < 0.0001					
EIV.N (G)	(Intercept)	3.8553	0.3912	9.855	< 0.001
obs. = 47	log1p(Biomass)	0.4276	0.1023	4.179	< 0.001
AICc = 113.1	Age	-0.0080	0.0049	-1.649	0.0991
$AICc_0$ = 127.5					
Random effect SD:					
Year < 0.0001					
Forest District < 0.0001					
EIV.SR (G)	(Intercept)	3.6800	0.6081	6.051	< 0.001
obs. = 47	log1p(Biomass)	0.6887	0.1685	4.087	< 0.001
AICc = 149.9	Age	-0.0129	0.0071	-1.816	0.0694
$AICc_0$ = 165.5					

Random effect SD: Year = 0.2472 Forest District = 0.0001					
SLA (G) obs. = 47 AICc = 490 $AICc_0$ = 491	(Intercept)	212.5070	5.9510	35.710	< 0.001
Random effect SD: Year = 0.001714 Forest District = 0.0004					
H (G)	(Intercept)	0.4551	0.1082	4.206	< 0.001
obs. = 47	log1p(Biomass)	0.1941	0.0556	3.493	0.0005
AICc = 44.8 $AICc_0$ = 55.3					
Random effect SD: Year < 0.0001 Forest District = 0.1082					
SM (G) obs. = 47 AICc = 72.3 $AICc_0$ = 73.3	(Intercept)	1.5620	0.0777	20.100	< 0.001
Random effect SD: Year = 0.0419 Forest District < 0.0001					

Abbreviations: **SE** – standard error; **z** – z-test statistic; **Pr(>|z|)** – p-value; **AICc** – Akaike's Information Criterion; **$AICc_0$** – AICc of null model; **SD** – standard deviation; **P** – Poisson distribution; **G ─** Gaussian distribution; **FRic ─** SES Functional richness; **FDis ─** SES Functional dispersion; **PD ─** Faith's phylogenetic diversity; **MPD ─** Mean Pairwise Distance; **rich ─** Species richness; **shan ─** Shannon's diversity index; **EIV.L ─** Light Ecological Indicator Value; **EIV.M ─** Moisture Ecological Indicator Value; **EIV.N ─** Soil Fertility Ecological Indicator Value; **EIV.SR ─** Soil Reaction Ecological Indicator Value; **SLA ─** Specific Leaf Area CWM [$cm^2\ g^{-1}$]; **H ─** Maximum height CWM [m]; **SM ─** Seed mass CWM [mg]

Table S21. The parameters of Generalized Linear Mixed-Effect Models for the impact of *P. serotina* aboveground biomass (AB) on different plant diversity indicators on nutrient-rich sites in summer. Abbreviation in parentheses for each species indicates the distribution of dependent variable.

Response	Variable	Estimate	SE	z	Pr(>|z|)
rich (NB)	(Intercept)	2.9926	0.0408	73.370	< 0.001
obs. = 48					
AICc = 310.6					
$AICc_0$ = 311.6					
Random effect SD:					
Year < 0.0001					
Forest District < 0.0001					
shan (G)	(Intercept)	1.8099	0.0727	24.880	< 0.001
obs. = 48					
AICc = 62.1					
$AICc_0$ = 63					
Random effect SD:					
Year = 0.0668					
Forest District < 0.0001					
FRic (G)	(Intercept)	-0.5959	0.2351	-2.535	0.0112
obs. = 48					
AICc = 134.5					
$AICc_0$ = 135.4					
Random effect SD:					
Year = 0.3351					
Forest District < 0.0001					
FDis (G)	(Intercept)	0.4938	0.3287	1.502	0.1330
obs. = 48	Age	-0.0073	0.0034	-2.147	0.0318
AICc = 118.2					
$AICc_0$ = 121.4					
Random effect SD:					
Year < 0.0001					
Forest District < 0.0001					
PD (G)	(Intercept)	-0.1570	0.1104	-1.422	0.1550
obs. = 48					
AICc = 118.5					
$AICc_0$ = 119.4					
Random effect SD:					
Year < 0.0001					
Forest District < 0.0001					
MPD (G)	(Intercept)	0.4720	0.3958	1.192	0.2331
obs. = 48	Age	-0.0084	0.0037	-2.262	0.0237
AICc = 118.4					

$AICc_0$ = 122.3					
Random effect SD:					
Year < 0.0001					
Forest District = 0.3429					
EIV.L (G)	(Intercept)	5.0259	0.1077	46.670	< 0.001
obs. = 48					
AICc = 104.3					
$AICc_0$ = 105.3					
Random effect SD:					
Year < 0.0001					
Forest District = 0.0577					
EIV.M (G)	(Intercept)	5.1445	0.0683	75.330	< 0.001
obs. = 48					
AICc = 1.3					
$AICc_0$ = 2.3					
Random effect SD:					
Year < 0.0001					
Forest District = 0.1248					
EIV.N (G)	(Intercept)	5.7040	0.2430	23.470	< 0.001
obs. = 48					
AICc = 121.2					
$AICc_0$ = 122.2					
Random effect SD:					
Year < 0.0001					
Forest District = 0.4381					
EIV.SR (G)	(Intercept)	5.1457	0.4463	11.529	< 0.001
obs. = 48	Age	0.0088	0.0042	2.108	0.0350
AICc = 127.9					
$AICc_0$ = 131.1					
Random effect SD:					
Year < 0.0001					
Forest District = 0.4075					
SLA (G)	(Intercept)	137.6755	59.4388	2.316	0.0205
obs. = 48	log1p(Biomass)	34.6041	17.9909	1.923	0.0544
AICc = 614.7	Age	2.5209	0.6027	4.183	< 0.001
$AICc_0$ = 628.7					
Random effect SD:					
Year = 0.0056					
Forest District < 0.0001					

H (G)	(Intercept)	0.8121	0.1420	5.717	< 0.001
obs. = 48	log1p(Biomass)	0.0809	0.0430	1.882	0.0599
AICc = 37.2	Age	-0.0026	0.0014	-1.788	0.0737
$AICc_0$ = 39.8					
Random effect SD:					
Year < 0.0001					
Forest District < 0.0001					
SM (G)	(Intercept)	1.4689	0.1000	14.720	< 0.001
obs. = 48					
AICc = 64.2					
$AICc_0$ = 65.1					
Random effect SD:					
Year < 0.0001					
Forest District = 0.1519					

Abbreviations: **SE** – standard error; **z** – z-test statistic; **Pr(>|z|)** – p-value; **AICc** – Akaike's Information Criterion; **$AICc_0$** – AICc of null model; **SD** – standard deviation; **NB** – negative binomial distribution; **G ─** Gaussian distribution; **FRic ─** SES Functional richness; **FDis ─** SES Functional dispersion; **PD ─** Faith's phylogenetic diversity; **MPD ─** Mean Pairwise Distance; **rich ─** Species richness; **shan ─** Shannon's diversity index; **EIV.L ─** Light Ecological Indicator Value; **EIV.M ─** Moisture Ecological Indicator Value; **EIV.N ─** Soil Fertility Ecological Indicator Value; **EIV.SR ─** Soil Reaction Ecological Indicator Value; **SLA ─** Specific Leaf Area CWM [$cm^2\ g^{-1}$]; **H ─** Maximum height CWM [m]; **SM ─** Seed mass CWM [mg]

References

Alberti G, Candido P, Peressotti A, Turco S, Piussi P, Zerbi G (2005) Aboveground biomass relationships for mixed ash (*Fraxinus excelsior* L. and *Ulmus glabra* Hudson) stands in Eastern Prealps of Friuli Venezia Giulia (Italy). Annals of Forest Science 62: 831–836. https://doi.org/10.1051/forest:2005089

Baker M, King R, Kahle D (2020) An Introduction to TITAN2. Version 2.4.3. https://CRAN.R-project.org/package=TITAN2

Brown JK (1976) Estimating shrub biomass from basal stem diameters. Canadian Journal of Forest Research: 153–158. https://doi.org/10.1139/x76-019

Bury S, Dyderski MK (2025a) Invasive *Prunus serotina* vs. *Robinia pseudoacacia*: How does temperate forest natural regeneration respond to their quantity? NeoBiota 97: 179–213. https://doi.org/10.3897/neobiota.97.135421

Forrester DI, Tachauer IHH, Annighoefer P, Barbeito I, Pretzsch H, Ruiz-Peinado R, Stark H, Vacchiano G, Zlatanov T, Chakraborty T, Saha S, Sileshi GW (2017) Generalized biomass and leaf area allometric equations for European tree species incorporating stand structure, tree age and climate. Forest Ecology and Management 396: 160–175. https://doi.org/10.1016/j.foreco.2017.04.011

Jagodziński A, Dyderski M, Gęsikiewicz K, Horodecki P (2018) Tree- and Stand-Level Biomass Estimation in a *Larix decidua* Mill. Chronosequence. Forests 9: 587. https://doi.org/10.3390/f9100587

Jagodziński AM, Dyderski MK, Gęsikiewicz K, Horodecki P (2019) Effects of stand features on aboveground biomass and biomass conversion and expansion factors based on a *Pinus sylvestris* L. chronosequence in Western Poland. European Journal of Forest Research 138: 673–683. https://doi.org/10.1007/s10342-019-01197-z

Zasada M (2017) Raport końcowy z tematu badawczego “Ekologiczne, gospodarcze i urządzeniowe konsekwencje występowania wybranych gatunków drzew obcych w Polsce” realizowanego w latach 2013-2017 przez Samodzielną Pracownię Dendrometrii i Nauki o Produkcyjności Lasu na zlecenie Dyrekcji Generalnej Lasów Państwowych w Warszawie. SGGW, Warszawa