



*Patryk Czortek\**, *Szymon Świącicki*, *Marcin K. Dyderski*,  
*Marcin T. Mazurkiewicz*, *Kamil Kisło*, *Przemysław Kurek*,  
*Kamil K. Morawski*, *Andrzej Zalewski*, *Ewa Komar*

## Raccoon dogs surpass invasive cherry plum *Prunus cerasifera* Ehrh. fruit removal over native mammals in the Białowieża Forest

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**Abstract:** Multiple biological invasions lead to the emergence of novel associations between non-native species in their secondary range. Such interactions often result in mutual facilitation for both species and can promote the further spread of non-native organisms.

We assessed the role of an invasive mammal in shaping the dispersal dynamics of an invasive tree within a primeval temperate forest landscape.

We used an example of raccoon dog (*Nyctereutes procyonoides* Gray) and cherry plum *Prunus cerasifera* Ehrh. in the Białowieża Forest (NE Poland). Using camera traps, we investigated animals feeding on cherry plum fruits offered in 15 study plots.

The mean time raccoon dogs spent in plots was approximately 13-fold greater than that recorded for native mammal species, particularly in invasion and double-control plots. The probability of raccoon dog presence increased over time in control but remained stable in invaded and double-control plots. Fruit removal increased with raccoon dog visitation time and was relatively similarly high across all three treatments.

Even in well-preserved landscapes with almost intact native mammal community, two invasive species can quickly develop novel associations, in <60 years of coexistence. This process may lead to a more effective spread of cherry plum, which recently entered the best preserved part of the Białowieża Forest. Our study is the first evidence that these interactions can also develop in landscapes isolated from high human impact. Therefore, the next introductions of new, non-native species, can result in unpredictable effects, accelerating each other spread and increasing their impacts on native ecosystems' functioning.

**Keywords:** endozoochory, nonnative species interactions, *Nyctereutes procyonoides*, oak-hornbeam forest, *Prunus cerasifera*

**Addresses:** P. Czortek, Sz. Świącicki, M. T. Mazurkiewicz, K. Kisło, University of Warsaw, Faculty of Biology, Białowieża Geobotanical Station, Sportowa 19, 17-230 Białowieża, Poland, e-mail: [p.czortek@biol.uw.edu.pl](mailto:p.czortek@biol.uw.edu.pl)

M. K. Dyderski, P. Kurek, Adam Mickiewicz University in Poznań, Department of Systematic and Environmental Botany, Faculty of Biology, Uniwersytetu Poznańskiego 6, 61-614 Poznań, Poland  
K. K. Morawski, A. Zalewski, E. Komar, Polish Academy of Sciences, Mammal Research Institute, Stoczek 1, 17-230 Białowieża, Poland

\* corresponding author

## Introduction

The introduction of species in new range and their subsequent colonisation of new areas has continued to increase in this century (Pyšek et al., 2020). The process of successive invasion is linked to a number of factors, including life history of invasive species, ecosystem types or disturbances, propagule pressure, and synergistic effects among non-natives (Simberloff & Von Holle, 1999; Tedeschi et al., 2025). These reinforcing interactions refer to processes where the establishment or activity of one non-native species facilitates the spread, persistence, or ecological success of others (Daly et al., 2023). They result in novel invasion-driven feedbacks that may exert complex and far-reaching impacts on ecosystem functioning (Aizen & Torres, 2024; Tedeschi et al., 2025). One key pathway through which invasive species can reinforce each other is the beneficial facilitation between fleshy-fruited invasive plant species and invasive frugivores (Vergara-Tabares et al., 2015). Numerous invasive trees and shrubs produce abundant, energetically rich fruits that are readily consumed by generalist animals, including non-native birds and mammals, which may act as effective seed dispersers through endozoochory (Bobadilla et al., 2023). These reciprocal relationships not only facilitate the persistence and spread of non-native plants but also enhance the population density and migration abilities of frugivore invaders, thus increasing their invasiveness (Tedeschi et al., 2022; Traveset & Richardson, 2014).

Although more than 66% of the most widespread invasive woody plants worldwide have fleshy fruits or attract animal dispersers by other fruit structures (Traveset & Richardson, 2014), only a few case studies have described or confirmed seed dispersal of invasive plant species by non-native mammals. Such cases have been documented, for example, on Mediterranean islands (Bourgeois et al., 2005; López-Darias & Nogales, 2008; Padrón et al., 2011), in semiarid regions of Argentina (Bobadilla et al., 2016, 2020), or in Hawaiian forests (Shiels & Drake, 2011). Positive feedbacks promoting invasive plant success via enhanced seed dispersal have been reported in highly human-altered ecosystems (e.g., Bobadilla et al., 2016; Bourgeois et al., 2005; López-Darias & Nogales, 2008; Padrón et al., 2011), while not assessed in more natural landscapes, with high native biodiversity and well-established complex trophic interactions.

Low human impact forest landscapes with a largely intact native mammal community have traditionally been considered relatively resistant to invasions due to their dense canopies, stable microclimates, and high structural complexity, which create strong biotic barriers to non-native plant species (Martin

et al., 2009; Simberloff et al., 2002). However, these defence mechanisms may be weakened by the introduction of animal invaders able to modify the environment in ways that facilitate the establishment of subsequent plant invaders, leading to synergistic effects among non-native species (Corenblit et al., 2014; Crooks, 2002). Therefore, understanding the complex interactions between invasive plants and animals, particularly those involved in seed dispersal and endozoochory (Kurek et al., 2024), is crucial for assessing the long-term ecological impacts of biological invasions in forest landscapes, especially in areas of high conservation value.

In the Białowieża Forest, the invasive cherry plum (*Prunus cerasifera* Ehrh.) is one of the few non-native species producing fleshy fruits, offering a potential food resource for vertebrate frugivores (Kurek, 2015; Castañeda et al., 2018). Native to southeastern Europe and western-central Asia, it establishes across a wide range of conditions beyond its natural range, including ruderal habitats, shrublands, forest edges, and forest interiors (see Czortek et al., 2024 for a review). Although present in the Białowieża Forest for over 60 years (Smirnov, 1965; Adamowski et al., 2002), its dispersal pathways and ecological impact remain poorly understood. *Prunus cerasifera* can alter understory community assembly rules and successional trajectories of oak-hornbeam forests (Czortek et al., 2025a). Moreover, it can shift epiphytic bryophyte assemblages towards pioneer, light-demanding species (Czortek et al., 2025b), and alter lichen communities, accelerating their succession (Łubek et al., 2025).

Similarly to non-native fleshy-fruited trees, the pool of invasive vertebrates in the Białowieża Forest is limited. Among the non-native mammals recorded in the region, only the raccoon dog (*Nyctereutes procyonoides* Gray) is a terrestrial, omnivorous species whose diet and habitat use make it a plausible consumer of fleshy fruits from non-native trees and a potential seed disperser (Kurek et al., 2024; Majewski et al., 2026). In contrast, the other invasive mammals are mainly aquatic (e.g. muskrat *Ondatra zibethicus* L., or American mink *Neovison vison* (Schreber)), and thus unlikely to interact with fruiting woody plants. The raccoon dog is a widely distributed invasive canid in Europe (Tedeschi et al., 2022; Majewski et al., 2026), native to the Far East of Asia (Laurimaa et al., 2016). Its invasion success is associated with broad environmental tolerance, high reproductive output, and an opportunistic omnivorous diet (Kauhala et al., 1998; Kauhala & Kowalczyk, 2011; Nowakowski et al., 2020; Majewski et al., 2026). Its spread has been facilitated by multiple large-scale introductions, enhancing genetic diversity, and maintaining gene flow among populations (Kauhala & Kowalczyk, 2011; Majewski et al., 2026).

The species is considered to negatively affect native fauna through predation and competition with native mesocarnivores (see Kauhala & Kowalczyk, 2011 for a review). It serves as a reservoir and vector of zoonotic parasites, including *Echinococcus multilocularis* and *Trichinella* spp. (Laurimaa et al., 2016).

The raccoon dog has been present in the Białowieża Forest for over 70 years (Dehnel, 1956; Nowak & Pielowski, 1964), a time span sufficient for population establishment, range stabilization, and integration into local trophic networks. This period largely overlaps with the spread of *P. cerasifera*, thereby facilitating the emergence of novel interspecific interactions between co-occurring invasive species. Moreover, ongoing climate change may potentially favour both species (Kochmann et al., 2021; Tedeschi et al., 2025; Czortek et al., 2026), promoting their spread across newly suitable areas (Brzeziński et al., 2019; Majewski et al., 2026). Thus, a focus on the novel ecosystem services provided by invasive fleshy-fruited trees, together with the role of invasive animals in their dispersal, highlights a critical but often overlooked mechanism that may increase the invasibility of close-to-natural forests (Simberloff et al., 2002; Martin et al., 2009; Kuebbing, 2020; Tedeschi et al., 2022). Therefore, the aim of this study was to identify the assemblage of dispersal vectors of cherry plum and to assess the potential for its further spread in near-natural forest ecosystem, with special emphasis on the invasive raccoon dog.

We hypothesized that raccoon dog would play a disproportionately important role in the dispersal of invasive cherry plum. The importance of this opportunistic omnivore in the spread of *P. cerasifera* may depend on its behavioural traits and ecological flexibility (Kochmann et al., 2021; Tedeschi et al., 2025). While native animals are typically embedded in stable food webs (Jędrzejewska & Jędrzejewski, 1998), the raccoon dog may more readily incorporate novel fruit sources into its diet. Alternatively, we hypothesized that cherry plum will be consumed by all native and invasive mammals in similar proportions, and the differences will only be due to density and habitat selectivity between them. To test research hypotheses, we conducted an experiment in early successional stages of oak-hornbeam forests developing on two clearings encircled by the Białowieża Primeval Forest. One of the glades is already undergoing invasion and serves as a propagule source of cherry plum for the adjacent primeval forest ecosystem (Czortek et al., 2024; Czortek et al., 2025a), while the other remains free of cherry plum individuals. We experimentally offered cherry plum fruits in both glades and monitored their consumption by animals.

## Methods

### Study area

The study was conducted at two open areas located in the Białowieża Forest region: Białowieża Clearing (13.5 km<sup>2</sup>, with a village of ~1,800 inhabitants) and Budy Clearing (5.5 km<sup>2</sup>; ~100 inhabitants). Both are located approximately 10 km apart from each other and enclosed by the Białowieża Primeval Forest (Fig. 1). The clearings have a long history of mowing, grazing, and agriculture, beginning in the 17<sup>th</sup> and 18<sup>th</sup> centuries and lasting till the 1950s. Land abandonment intensified in the early 1990s. Both clearings are situated within the Natura 2000 site “Białowieża Forest”, where current human activities are limited to mowing on semi-natural meadows. Relatively large parts of both clearings are dominated by the early stages of subcontinental oak-hornbeam forest (*Tilio-Carpinetum*), with the tree stand composed of silver birch *Betula pendula*, European hornbeam *Carpinus betulus*, European aspen *Populus tremula*, pedunculate oak *Quercus robur*, goat willow *Salix caprea*, and small-leaved lime *Tilia cordata*. The cherry plum is limited to the northern part of the Białowieża Clearing, where it locally dominates early successional forest patches, often comprising up to 90% of canopy cover (Czortek et al., 2025a), but is absent in the Budy Clearing.

### Experimental design

We conducted a field experiment to examine which animal species consume the fruits of cherry plum in natural conditions, and whether their interest differs depending on the presence of cherry plum trees in the environment. The experiment was carried out from August 22 for 14 days, coinciding with the natural fruiting period of *P. cerasifera* in the region. This timing ensured ecologically realistic conditions. The study area was characterized by low availability of fleshy fruit trees and shrubs, and no other fruiting species were present during the experiment, minimizing the possibility that animals selected among alternative fruit resources. Moreover, the relatively short duration of the experiment minimized the potential risk of unintentionally facilitating the spread of *P. cerasifera* through fruit provisioning.

Fruits were placed on the ground in early successional patches of *Tilio-Carpinetum* forest, with similar native tree species composing their canopies. We established three types of plots: (1) ‘invasion’ plots, located in clearing colonized by cherry plum (Białowieża) in patches where cherry plum trees were present, (2) ‘control’ plots, located in clearing colonized by cherry plum (Białowieża) but in patches without fruiting cherry plum trees, and

(3) ‘double-control’ plots situated on clearing where the cherry plum has not been recorded at all (Budy) (Fig. 1). Both ‘invasion’ and ‘control’ plots were located within the Białowieża Clearing, while ‘double-control’ plots were situated in a separate site devoid of cherry plum (Budy Clearing). Each treatment included five replicate plots, resulting in a total of 15 study plots.

The number of plots was determined by the availability of locations that meet strict ecological criteria. Plot locations were selected to ensure similar structural conditions, and most importantly, to match the required tree species composition defined for each treatment. The selected forest patches were neither too sparse nor too dense, offering shelter for animals while allowing access to fruits. All plots were at least 90 meters away from the nearest human settlement (mean: 525 m), and on average 350 meters from the forest edge. To avoid potential pseudoreplication and spatial dependencies, plots were separated by a minimum distance of 300 meters and distributed as evenly as possible across both clearings, while also avoiding proximity to roads.

At each plot, 500 grams of freshly collected cherry plum fruits were placed daily in a shallow, flat orange plastic basket (35 × 25 cm), hereafter ‘basket’, positioned directly on the ground (Fig. 1). This relatively small quantity of fruit per plot was deliberately

used to reduce the likelihood of inadvertently promoting the dispersal of *P. cerasifera* via experimental fruit provisioning. The basket colour resembled the fruit colour to avoid attracting or deterring animals. Only ripe, healthy, and unspoiled fruits were used. Daily, we recorded the weight of the remaining fruits to estimate their percentage proportion removed by animals.

To document animal visits, we deployed a camera trap (Bushnell Trophy Cam HD Aggressor) at each plot. The cameras were mounted approximately 0.5 meters above ground, ~2 meters from the basket. The camera traps were programmed to capture a photo every second upon motion detection (triggered by temperature changes). Due to technical failures and one instance of theft, we lost 11 camera-days of data from 210 camera-days of exposition. The corresponding missing data were excluded from statistical analyses. All recorded photos were uploaded to Trapper, a web-based application for managing camera trap data (Bubnicki et al., 2016). A visit by an animal was defined as a sequence of photos separated by at least five minutes from the next sequence. This threshold was chosen to balance the independence of recorded events with the risk of merging distinct visits into a single record, as shorter intervals may over-split continuous activity whereas longer intervals may underestimate the number of independent visits (Meek

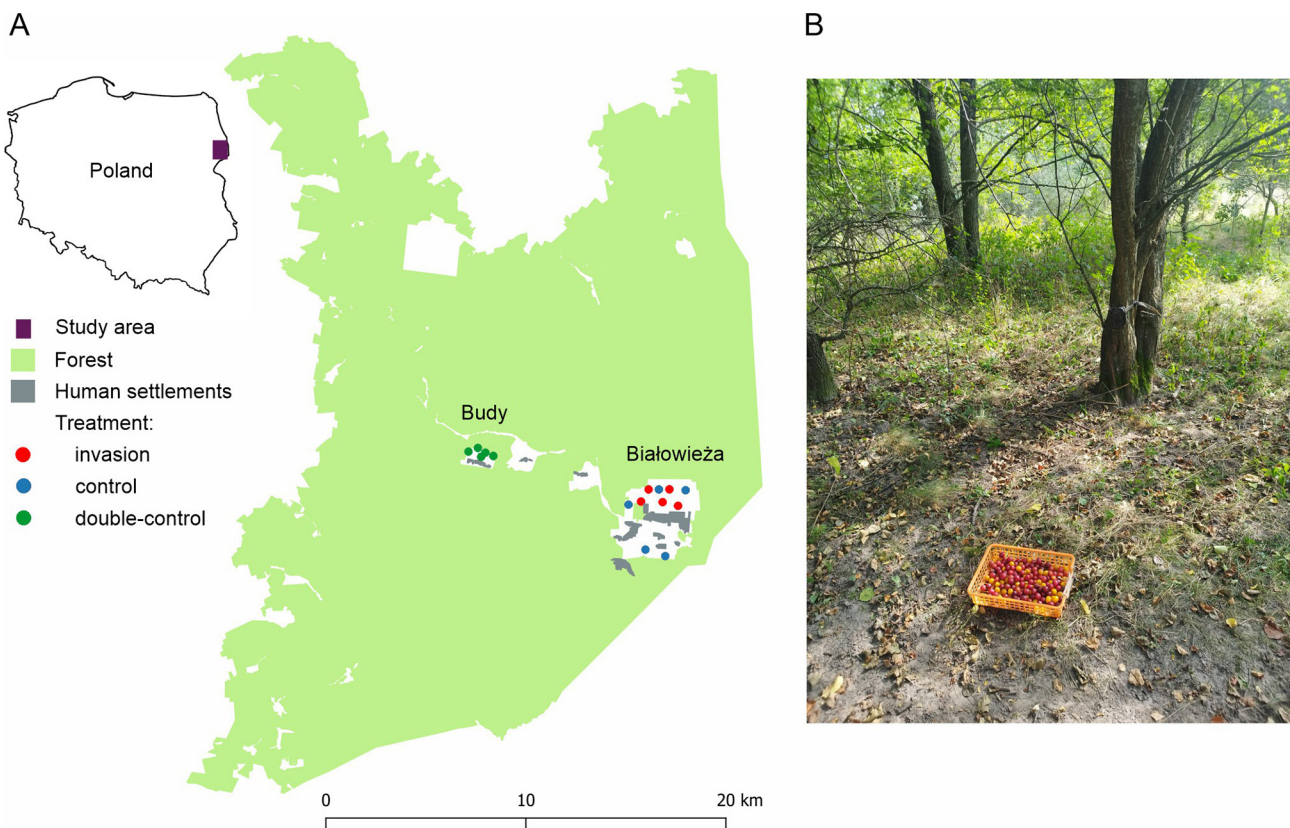


Fig. 1. Study area in the Białowieża Forest, north-eastern Poland, showing distribution of plots (A) with an example of study plot with a basket of cherry plum fruits (B)

et al., 2014). A single person (Sz. Ś.) classified the photos. Species and group size were determined for every recorded visit.

## Data analysis

To compare differences in time spent in plots by raccoon dog and other recorded mammal species, as well as among three treatments (i.e., invasion, control, and double-control plots), we used a mixed-effects linear model assuming a normal distribution of the response variable (*lmerTest::lmer()* function). In addition to additive effects, the model accounted for an interaction term between mammal species and treatment. To assess differences in the probability of raccoon dog presence in plots during the experiment duration and depending on treatments, we employed a generalized linear model assuming a binomial distribution of the response variable (*base::glm()* function). To evaluate the impact of time spent in plots by raccoon dog and to compare treatment effects on the percentage disappearance of cherry plum fruits, we employed a zero-inflated generalized mixed-effects model with a beta-distributed response variable and an intercept in the zero-inflation component (*glmmTMB::glmmTMB()* function). To account for potential variation in animal activity due to factors such as weather shifts during the experiment, we specified trap-day and plot identity as random effects in the first and third models built, and plot identity alone in the second model.

We adhere to the American Statistical Association's recommendations (Wasserstein & Lazar, 2016) and refrain from using *P*-values to assess the significance of results, since *P*-values' strong dependence on sample size can conceal biologically meaningful patterns. We applied the *emmeans::emmeans()* and *ggeffects::ggpredict()* functions to calculate marginal responses while illustrating the models' results, which depict predicted values with all other explanatory variables held at their mean (constant) levels. We conducted all statistical analyses in R version 4.3.0 ("Already Tomorrow"; R Core Team, 2025).

## Results

A total of 540 animal visits were recorded during the 14 days of the experiment. The six most frequently observed species included raccoon dog, pine marten (*Martes martes* L.), European badger (*Meles meles* L.), red deer (*Cervus elaphus* L.), red fox (*Vulpes vulpes* L.), and a group of unidentified rodent species. These six species were included in analyses, with raccoon dog accounting for the highest number of observations (Table 1).

Table 1. Number of visits and total time spent in plots by species

Species/group of species	Number of visits	Time spent [s]
Raccoon dog ( <i>Nyctereutes procyonoides</i> Gray)	368	58462
Pine marten ( <i>Martes martes</i> L.)	36	3855
Rodents (unidentified)	34	1762
European badger ( <i>Meles meles</i> L.)	31	4585
Red deer ( <i>Cervus elaphus</i> L.)	29	5188
Red fox ( <i>Vulpes vulpes</i> L.)	21	441
Roe deer ( <i>Capreolus capreolus</i> L.)	8	668
European bison ( <i>Bison bonasus</i> L.)	5	97
Domestic cat ( <i>Felis catus</i> L.)	4	185
Wolf ( <i>Canis lupus</i> L.)	2	76
Birds (unidentified)	2	3

The parameters of all models performed are presented in Table 2. The mean time that raccoon dogs spent in plots (295 s) was approximately 13-fold longer than that recorded for red deer, European badger, and pine marten (26 s, 23 s, and 20 s, respectively). Rodents and red fox revealed the lowest mean time durations spent in plots (9 s and 3 s, respectively; Fig. 2a). All recorded mammals spent comparable time durations in invasion and double-control plots (79 s and 74 s, respectively), whereas their time on control plots was approximately half as long (36 s; Fig. 2b). Raccoon dog followed the same pattern, spending the same time in invasion and double-control plots ( $358 \pm 28$  SE s), but on control plots it spent about 50% less time (168 s; Fig. 2c).

The probability of raccoon dog presence remained unchanged in invasion plots throughout the experiment, whereas it showed a slight increase in double-control plots (from 62% on day 1 to 73% on day 14) and a pronounced increase in control plots (from 22% to 60% over the same period; Fig. 3a). The proportion of cherry plum fruits disappearance increased from 51% to 96% as time spent in plots by raccoon dog ranged from 0 to 1600 s (Fig. 3b). Mean percentage of disappearing fruits reached its highest value in invasion plots (65%), and was 11% and 8% higher compared to control and double-control plots, respectively (Fig. 3c).

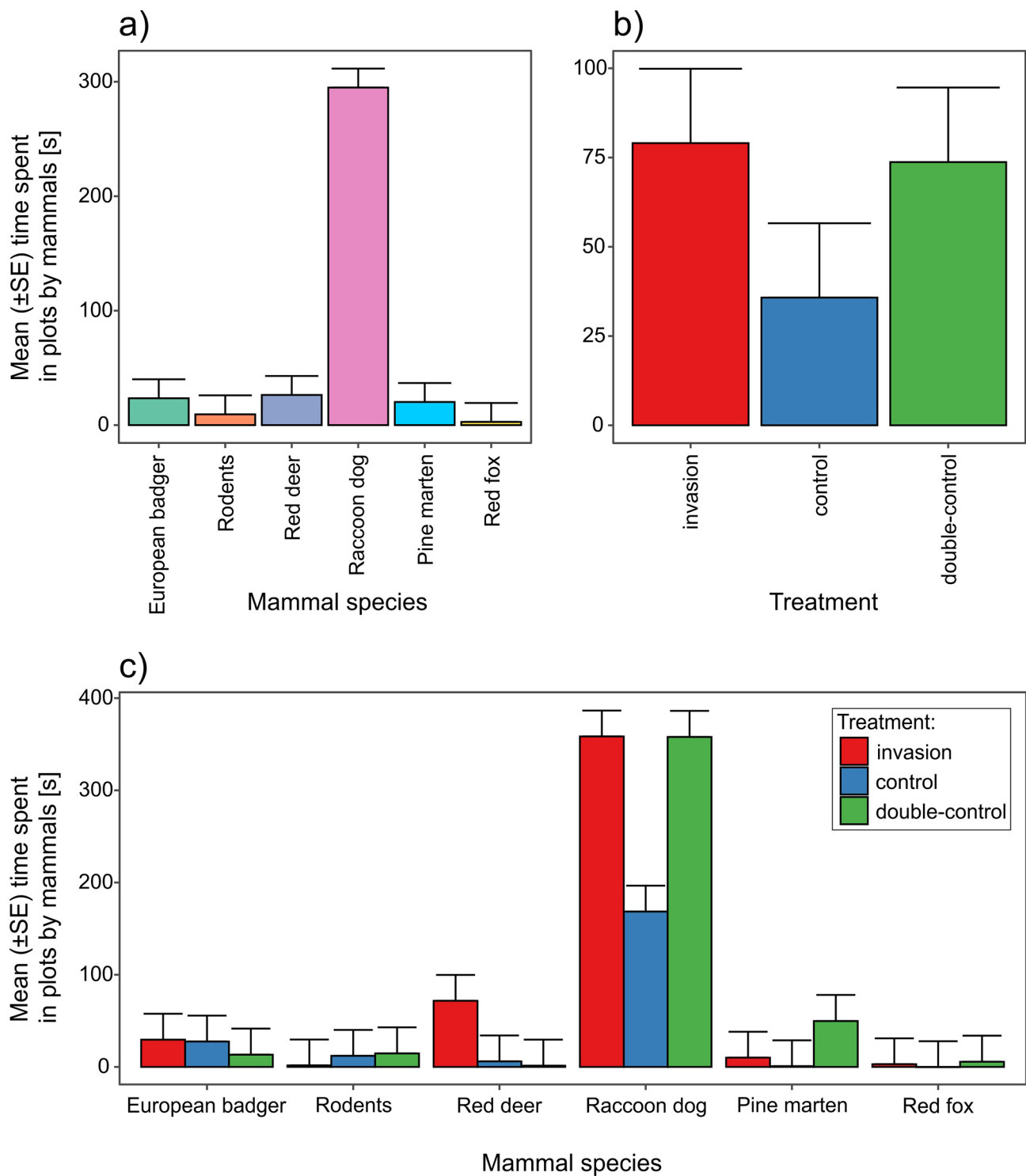


Fig. 2. Visualisation of linear mixed-effect model showing differences in mean ( $\pm$ SE) time spent in plots by Raccoon dogs and other recorded mammal species (a), differences in mean ( $\pm$ SE) time spent by all recorded mammals among treatments (b), and accounting for interaction between mammal species and treatment (c). For model parameters see Table 2

Table 2. Parameters of mixed effect models testing for: differences in time spent in plots by invasive raccoon dogs and recorded native mammal species depending on treatments (a), differences in probability of raccoon dog presence in plots during the experiment duration and depending on treatments (b), and effects of time spent in plots by raccoon dogs and differences among treatment effects on the percentage disappearance of *P. cerasifera* fruits (c). RE SD – SD of random effects

Predictor	Estimate	SE	t/z	P	RE SD
a) Time spent by mammal species [s]					
Intercept	27.540	28.089	0.980	0.333	Plot id = 41.590
Species = Rodents	-15.507	29.201	-0.531	0.595	Trap-day = 15.110
Species = Reed deer	-21.522	29.201	-0.737	0.461	
Species = Raccoon dog	140.955	29.201	4.827	<0.001	
Species = Pine marten	-26.791	29.201	-0.917	0.359	
Species = Red fox	-27.746	29.201	-0.950	0.342	
Treatment = double-control	-14.298	39.478	-0.362	0.719	
Treatment = invasion	2.030	39.310	0.052	0.959	
Rodents: double-control	16.877	41.612	0.406	0.685	
Rodents: invasion	-12.448	41.296	-0.301	0.763	
Reed deer: double-control	9.553	41.612	0.230	0.818	
Reed deer: invasion	63.657	41.296	1.541	0.123	
Raccoon dog: double-control	203.660	41.612	4.894	<0.001	
Raccoon dog: invasion	187.896	41.296	4.550	<0.001	
Pine marten: double-control	63.314	41.612	1.522	0.128	
Pine marten: invasion	7.254	41.296	0.176	0.861	
Red fox: double-control	20.069	41.612	0.482	0.630	
Red fox: invasion	1.090	41.296	0.026	0.979	
b) Probability of raccoon dog presence in plots [%]					
Intercept	0.646	0.555	1.164	0.244	Plot id = 1.672
Day of experiment	0.001	0.064	0.005	0.996	-
Treatment = control	-2.047	0.814	-2.513	0.012	
Treatment = double-control	-0.211	0.789	-0.268	0.789	
Day of experiment: control	0.127	0.097	1.373	0.170	
Day of experiment: double-control	0.040	0.092	0.432	0.666	
c) Proportion of fruits disappearance [%]					
Conditional model:					Plot id = 0.424
Intercept	0.052	0.325	0.162	0.872	Trap-day = 0.314
Time spent by Raccoon dogs	0.001	<0.001	5.682	<0.001	
Treatment = control	-0.443	0.413	-1.074	0.283	
Treatment = double-control	-0.338	0.375	-0.901	0.368	
Zero-inflation model:					
Intercept	-0.397	0.144	-2.747	0.006	

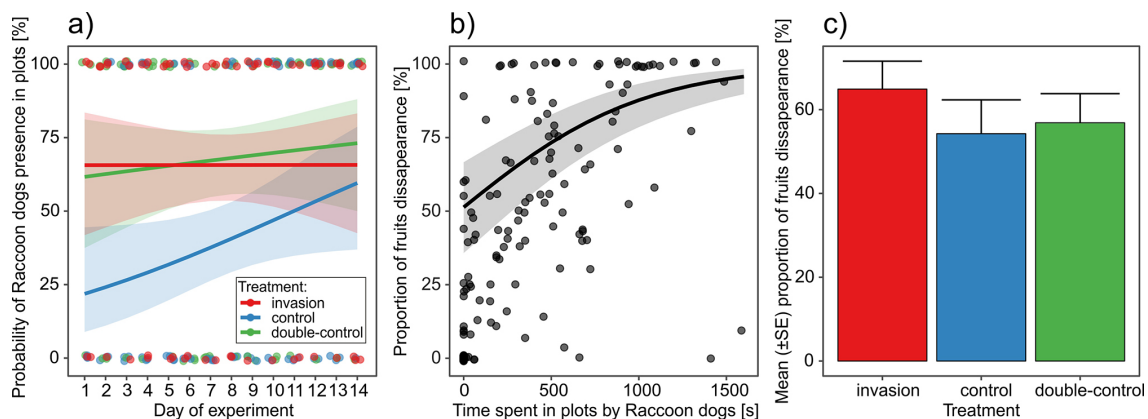


Fig. 3. Visualisation of generalized linear models assessing differences in the probability of raccoon dog presence in plots during the experiment duration and depending on treatments (a) and the impact of time spent in plots by raccoon dogs (b) with treatment effects on the percentage disappearance of cherry plum fruits (c). For model parameters see Table 2

## Discussion

### An invasive mammal is the main consumer of the invasive tree

Our study revealed that the fruits of the invasive cherry plum may be consumed by a relatively wide range of animals, suggesting a considerable variation in the fate of the fruits and, consequently, a high potential for drupe dispersal. Mammal species recorded at plots differ greatly in their morphology (e.g., body size), physiology (e.g., seed digestion efficiency, or seed-carrying capacity), ecology (e.g., home range size, movement behaviour or habitat preferences; Jędrzejewska & Jędrzejewski, 1998), and food-handling strategies (e.g., hoarding or immediate consumption), which may influence both the distance and success of seed dispersal (Delibes et al., 2019). Contrary to our second hypothesis, but in line with the first, the raccoon dog, an invasive species in Central Europe, was the most abundant visitor to the experimental plots, outnumbering all other animals.

All the four mesocarnivorous species visiting the study plots can be potentially considered as the main dispersers of cherry plum seeds, based on their size and food habits. Moreover, all of them are opportunistic omnivores, and fruits constitute a regular part of their diet (Fedriani et al., 2018; González-Varo et al., 2013; Hisano et al., 2016; Kurek, 2015; Kurek et al., 2024; Pagh et al., 2025). One would therefore expect a relatively high and similar presence of all these carnivore species on our experimental plots. However, the role of native frugivorous carnivores in cherry plum dispersal appears to be more limited, likely due to their dietary specialization and ecological constraints. Among these species, the raccoon dog stands out as the most frugivorous, with fruits reported up to 77% of diet frequency in some populations (Baltrūnaitė, 2006; Drygala et al., 2000; Kauhala et al., 1998; Kauhala & Kowalczyk, 2011; Pagh et al., 2025; Sidorovich et al., 2000, 2008; Sutor et al., 2010). In comparison, the average fruit content in the summer diet of native species reaches approximately 21–39% (Castañeda et al., 2022; Goszczyński et al., 2000; Mulder, 2012; Zalewski, 2005). Several other factors may also explain the comparatively low consumption of cherry plum fruits mammals, particularly rodents (Castañeda et al., 2022). Although it is also known to consume fruits, these typically may constitute a minor component of its diet, especially in landscapes of the Białowieża Forest (Jędrzejewska & Jędrzejewski, 1998). Pine martens, though frugivorous in late summer, were rarely detected in our plots, which may be due to their strong preference for mature forest (Wereszczuk & Zalewski, 2015). These environments provide essential vertical structure for escape from predators, a key element of

pine martens' ecology, and open clearings may thus be less attractive to them (Wereszczuk & Zalewski, 2015). European badger, despite having a broad diet that includes fruits, relies heavily on earthworms and other soil invertebrates (Goszczyński et al., 2000; Kowalczyk et al., 2003). Although both European badger and raccoon dog engage in seasonal fattening, their foraging behaviour differs. Raccoon dogs may consume fruits more frequently than badgers (Elmeros et al., 2018), preferring large-seeded fleshy fruits (Takatsuki et al., 2018). They may exhibit greater spatial flexibility (Drygala et al., 2008) and foraging boldness than European badger. The diet composition of raccoon dogs varies with season and landscape structure (Sutor et al., 2010). Such dietary flexibility is considered a key prerequisite for their success (Caut et al., 2008), enabling them to exploit sugar-rich fruiting patches, such as those of the cherry plum, more effectively than the European badger.

Nevertheless, even when taking the dietary and habitat differences into account, the disproportionately high frequency of raccoon dog presence in the study plots remains striking. This is especially surprising given that its population density in the Białowieża Forest region is not substantially higher than that of native species. In the Białowieża Forest, raccoon dog's population density ranges from 0.2 to 0.5 individuals per km<sup>2</sup> (Jędrzejewska & Jędrzejewski, 1998; Kowalczyk et al., 2008), which is comparable to that of native carnivores in the region, including the pine marten (0.5 individuals km<sup>-2</sup>), European badger (0.2 individuals km<sup>-2</sup>), and red fox (0.1 individuals km<sup>-2</sup>) (Jędrzejewska & Jędrzejewski, 1998; Kowalczyk et al., 2003, 2008). Based on these densities, we might expect a two- or threefold higher visitation rate at most, not a 13-fold one as our results revealed.

### Plasticity as a novel weapon of invasive animal

Native species have adapted to local conditions of food availability, and, in the absence of resource scarcity, may have limited incentive to explore or incorporate novel food sources (Labbé & King, 2020). In contrast, invasive species often display greater dietary plasticity and behavioural boldness, allowing them to exploit unfamiliar resources more readily (Griffin et al., 2022; Sol et al., 2014; Wright et al., 2010). While numerous animals are generally cautious and slow to recognize new items in their environment as edible, invasive species may be under stronger selective pressure to quickly identify and utilize novel food sources to become a successful invader (Sol et al., 2014). In our study, the invasive raccoon dogs appear to have successfully learned to exploit cherry

plum as a valuable food resource. In areas completely devoid of cherry plum, raccoon dogs appeared at experimental plots from the very beginning – at levels comparable to those in invaded and known areas. This suggests great spatial flexibility and foraging boldness, as well as remarkable capacity for rapid learning and recognition of novel food resources. In areas already invaded by cherry plum, where the tree is already established and represents a known food source, raccoon dogs exploit known food patches systematically and consistently. In contrast, when fruits were introduced at new locations within those invaded areas, raccoon dogs were slower to explore and exploit these sites. This behaviour likely reflects an energy-saving strategy, with animals initially relying on familiar food patches (Mitchell & Powell, 2004). Frugivores are known to learn the spatial and temporal distribution of fruiting trees (Saracco et al., 2004) and to return to fruit sources more frequently during the fruiting season. In our study, raccoon dogs spent similar amounts of time at baskets located beneath known fruiting trees and in control plots situated far from the invaded area. Their quick detection of fruit under known (several years of fruiting) trees likely reflects memory-based foraging, while their immediate response to baskets placed far from fruiting trees sheds light on how animals perceive the spatial distribution of food sources. It also demonstrates that even unpredictable appearances of fruiting sites do not limit their use by an invasive mammal.

When a non-native tree offers a high-quality food resource and an invasive animal possesses the behavioural flexibility to rapidly recognize and exploit it, new ecological positive interactions can emerge swiftly (Simberloff & Von Holle, 1999). Such interactions may bypass the ecological barriers that typically constrain establishment and dispersal, allowing both species to benefit: the plant gains a reliable dispersal vector, while the animal secures an easily accessible, energy-rich food source (Bobadilla et al., 2020; Latham et al., 2017), that potentially is not or less exploited by native species. The ability to flexibly exploit a wide range of food types – and the behavioural boldness to recognize and utilize unfamiliar resources – may thus act as a “novel weapon” within an ecosystem in a focus (Callaway & Ridenour, 2004).

### Positive invasion feedbacks in the context of the ecosystem invasibility

Even in species-rich, low human impact forest landscapes, the introduction of two non-native species functionally distinct from the native biota can give rise to novel interactions. In our study, the raccoon dog emerged as a main disperser of cherry plum’s drupes, demonstrating the prominent ability

to quickly incorporate this novel food source into its diet. Although both species have been present in the region for about 60 years, their interaction through seed dispersal and the provision of nutrient-rich food has resulted in mutual facilitation. Carnivores, regarding their morphological features (mostly their simple digestive mechanism with no rumination), may defecate almost intact seeds (Pigozzi, 1992; Fedriani & Delibes, 2009), and a similar process may likely be attributed to raccoon dog (Drygala et al., 2000; Wooldridge et al., 2024). Moreover, the broad-scale movements of raccoon dogs, combined with their capacity to penetrate diverse habitats and foraging strategy (Drygala et al., 2000; Wooldridge et al., 2024), both within established territories and during post-breeding dispersal (up to 100 km; Sutor, 2008), enable long-distance transport of ingested drupes with intact pulp, potentially facilitating seed deposition across a wide range of environments (Drygala et al., 2000). This movement across habitat boundaries is particularly relevant in our study system, as cherry plum is still in the early stages of colonizing the best preserved part of the Białowieża Forest. However, it yet fruit within this forest interior (Czortek et al., 2024), meaning that the main propagule sources located in early-successional forest patches on the clearing play an important role in cherry plum invasion into primeval forest (Czortek et al., 2025a). Raccoon dog may therefore serve as important vector connecting these fruiting sources with primeval forest parts that are not yet colonized, potentially accelerating the species’ spread into new habitats.

### Study limitations

Interpretation of our results should take into account several constraints arising from the study design and the local environment variability. Our study was carried out during the peak fruiting period of *P. cerasifera*, which allowed us to observe interactions under conditions of naturally high fruit availability. Although focusing on the peak fruiting season provided realistic insights into the studied interaction when resources were most abundant, the observations came from a single two-week period in a single year. Therefore, our experiment does not represent year-to-year changes in fruiting levels, carnivore activity or broader mammal community dynamics, and we cannot determine whether the patterns we documented are stable through time or specific to the conditions of that particular season. Camera traps provided reliable information on visits and foraging time, but this approach did not allow us to follow what happens to the seeds after consumption. Direct evidence of seed survival and deposition would require additional approaches such as germination tests or analyses of scats. The study was also limited

to early-successional stands in two forest clearings, which represent only a portion of the habitats used by both species in the Białowieża Forest region. Differences in vegetation structure, food availability or the presence of other carnivores in surrounding habitats may influence fruit removal in ways that were not reflected in our study plots. These limitations point to the need for longer-term research that spans several fruiting seasons and a wider range of habitats to better understand the ecological consequences of emerging interaction between two invasive species.

## Conclusions

Our findings, obtained under low human impact conditions, shed new light on the prevailing view that novel species interactions are restricted to human-altered environments (Heger et al., 2019; Hobbs et al., 2006). They reveal that even primeval forests may be vulnerable to ecological transformations triggered by recent invasions occurring in their closest surroundings. Benefiting from easily accessible fruits, the raccoon dog may act as a reliable vector for cherry plum dispersion, increasing its propagule pressure and illustrating how novel trophic interactions can threaten native ecosystem functioning. Numerous non-native fleshy-fruited plants rely primarily on endozoochory for seed dispersal, and several are currently spreading from cultivation (Wiatrowska et al., 2023). Given the long lag phases (Kowarik, 1995) and lack of ecosystem saturation by these non-natives (Seebens et al., 2017), similar scenarios may become increasingly common. This finding challenges the notion of traditionally high biotic resistance of well-preserved forest landscapes with a largely intact native mammal community (Martin et al., 2009; Simberloff et al., 2002). Moreover, our findings underscore the importance of acknowledging and managing emerging interspecific interactions among non-native species. However, the reason why the invasion of cherry plum began 40 years after the onset of its coexistence with invasive mammal remains an open question.

## References

- Adamowski W, Dvorak L & Ramanjuk I (2002) Atlas of alien woody species of the Białowieża Primeval Forest. *Phytocoenosis. Suppl. Cartographiae Geobotanicae* 14: 1–301.
- Aizen MA & Torres A (2024) The Invasion Ecology of Mutualism. *Annual Review of Ecology, Evolution & Systematics* 55: 41–63. doi:10.1146/annurev-ecolsys-102622-031210.
- Baltrūnaitė L (2006) Diet and winter habitat use of the red fox, pine marten and raccoon dog in Dzūkija National Park, Lithuania. *Acta Zoologica Lituanica* 16: 46–53. doi:10.1080/13921657.2006.10512709.
- Bobadilla SY, Benitez VV & Guichón ML (2016) Asiatic *Callosciurus* squirrels as seed dispersers of exotic plants in the Pampas. *Current Zoology* 62: 215–219. doi:10.1093/cz/zow009.
- Bobadilla SY, Marchetta A, Dacar MA, Ojeda RA & Cuevas MF (2020) Food habits of European rabbit and its role as seed dispersal of two *Mosqueta* roses: Facilitation among non-native species in a semiarid protected area of Argentina? *Biological Invasions* 22: 1565–1571. doi:10.1007/s10530-020-02205-9.
- Bobadilla SY, Olivares ET, Jaksic FM, Ojeda RA & Cuevas MF (2023) European rabbit (*Oryctolagus cuniculus*) as seed disperser in arid ecotones of Argentina: Non-native herbivore facilitation of native and non-native plants. *Mammal Research* 68: 625–635. doi:10.1007/s13364-023-00712-3.
- Bourgeois K, Suehs CM, Vidal E & Médail F (2005) Invasional meltdown potential: Facilitation between introduced plants and mammals on French Mediterranean islands. *Écoscience* 12: 248–256. doi:10.2980/i1195-6860-12-2-248.1.
- Brzeziński M, Żmihorski M, Zarzycka A & Zalewski A (2019) Expansion and population dynamics of a non-native invasive species: the 40-year history of American mink colonisation of Poland. *Biological Invasions* 21: 531–545. doi:10.1007/s10530-018-1844-7.
- Bubnicki JW, Churski M & Kuijper DPJ (2016) TRAPPER: An open source web-based application to manage camera trapping projects. *Methods in Ecology and Evolution* 7: 1209–1216. doi:10.1111/2041-210X.12571.
- Castañeda I, Fedriani JM & Delibes M (2018) Potential of red deer (*Cervus elaphus*) to disperse viable seeds by spitting them from the cud. *Mammalian Biology* 90: 89–91. doi:10.1016/j.mambio.2017.10.004.
- Castañeda I, Doherty TS, Fleming PA, Stobo-Wilson AM, Woinarski JCZ & Newsome TM (2022) Variation in red fox *Vulpes vulpes* diet in five continents. *Mammal Review* 52: 328–342. doi:10.1111/mam.12292.
- Caut S, Angulo E & Courchamp F (2008) Dietary shift of an invasive predator: Rats, seabirds and sea turtles. *Journal of Applied Ecology* 45: 428–437. doi:10.1111/j.1365-2664.2007.01438.x.
- 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. doi:10.1002/rra.2618.

- Crooks JA (2002) Characterizing ecosystem-level consequences of biological invasions: The role of ecosystem engineers. *Oikos* 97: 153–166. doi:10.1034/j.1600-0706.2002.970201.x.
- 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: 633–647. doi:10.1007/s10530-023-03188-z.
- Czortek P, Adamowski W & Dyderski MK (2025a) Invasive *Prunus cerasifera* alters understory diversity in the early successional oak-hornbeam forests. *Biological Invasions* 27: 185. doi:10.1007/s10530-025-03640-2.
- Czortek P, Dyderski MK, Łubek A, Mazurkiewicz MT & Wierzcholska S (2025b) Do native trees support epiphytic bryophytes diversity better than nonnatives? *Neobiota* 100: 321–344. doi:10.3897/neobiota.100.154929.
- Czortek P, Adamowski W, Paż-Dyderska S, Puchalka S & Dyderski MK (2026) Projected niche shifts of invasive *Prunus cerasifera* under climate change scenarios and its consequences. *Plant Ecology* 227: 6. doi:10.1007/s11258-025-01576-0.
- Daly EZ, Chabrierie O, Massol F, Facon B, Hess MCM, Tasiemski A, Grandjean F, Chauvat M, Viard F, Forey E, Folcher L, Buisson E, Boivin T, Baltora-Rosset S, Ulmer R, Gibert P, Thiébaud G, Pantel JH, Heger T, Richardson DM & Renault D (2023) A synthesis of biological invasion hypotheses associated with the introduction–naturalisation–invasion continuum. *Oikos* 2023: e09645. doi:10.1111/oik.09645.
- Dehnel A (1956) New species of mammal in Polish fauna *Nyctereutes procyonoides* (Gray). *Chrońmy Przyrodę Ojczystą* 12: 17–21.
- Delibes M, Castañeda I & Fedriani JM (2019) Spitting seeds from the cud: a review of an endozoochory exclusive to ruminants. *Frontiers in Ecology and Evolution* 7: 265. doi:10.3389/fevo.2019.00265.
- Drygala F, Mix HM, Stier N & Roth M (2000) Preliminary findings from ecological studies of the raccoon dog (*Nyctereutes procyonoides*) in eastern Germany. *Zeitschrift für Ökologie und Naturschutz* 9: 147–152.
- Drygala F, Stier N, Zoller H, Mix HM, Bögelsack K & Roth M (2008) Spatial organisation and intra-specific relationship of the raccoon dog *Nyctereutes procyonoides* in Central Europe. *Wildlife Biology* 14: 457–466. doi:10.2981/0909-6396-14.4.457.
- Elmeros M, Mikkelsen DMG, Nørgaard LS, Pertoldi C, Jensen TH & Chriél M (2018) The diet of feral raccoon dog (*Nyctereutes procyonoides*) and native badger (*Meles meles*) and red fox (*Vulpes vulpes*) in Denmark. *Mammal Research* 63: 405–413. doi:10.1007/s13364-018-0372-2.
- Fedriani JM & Delibes M (2009) Seed dispersal in the Iberian pear, *Pyrus bourgaeana*: A role for infrequent mutualists. *Ecoscience* 16: 311–321. doi:10.2980/16-3-3253.
- Fedriani JM, Wiegand T, Ayllón D, Palomares F, Suárez-Esteban A & Grimm V (2018) Assisting seed dispersers to restore oldfields: An individual-based model of the interactions among badgers, foxes and Iberian pear trees. *Journal of Applied Ecology* 55: 600–611. doi:10.1111/1365-2664.13000.
- González-Varo JP, López-Bao JV & Guitián J (2013) Functional diversity among seed dispersal kernels generated by carnivorous mammals. *Journal of Animal Ecology* 82: 562–571. doi:10.1111/1365-2656.12024.
- Goszczyński J, Jędrzejewska B & Jędrzejewski W (2000) Diet composition of badgers (*Meles meles*) in a pristine forest and rural habitats of Poland compared to other European populations. *Journal of Zoology* 250: 495–505. doi:10.1111/j.1469-7998.2000.tb00792.x.
- Griffin AS, Peneaux C, Machovsky-Capuska GE & Guez D (2022) How alien species use cognition to discover, handle, taste, and adopt novel foods. *Current Opinion in Behavioral Sciences* 45: 101136. doi:10.1016/j.cobeha.2022.101136.
- Heger T, Bernard-Verdier M, Gessler A, Greenwood AD, Grossart H-P, Hilker M, Keinath S, Kowarik I, Kueffer C, Marquard E, Mülle J, Niemeier S, Onandia G, Petermann JS, Rillig MC, Rödel M-O, Saul W-C, Schittko C, Tockner K, Joshi J & Jeschke JM (2019) Towards an integrative, eco-evolutionary understanding of ecological novelty: studying and communicating interlinked effects of global change. *BioScience* 69: 888–899. doi:10.1093/biosci/biz095.
- Hisano M, Raichev EG, Peeva S, Tsunoda H, Newman C, Masuda R, Georgiev DM & Kaneko Y (2016) Comparing the summer diet of stone martens (*Martes foina*) in urban and natural habitats in Central Bulgaria. *Ethology Ecology & Evolution* 28: 295–311. doi:10.1080/03949370.2015.1048829.
- Hobbs RJ, Arico S, Aronson J, Baron JS, Bridgewater P, Cramer VA, Epstein PR, Ewel JJ, Klink CA, Lugo AE, Norton D, Ojima D, Richardson DM, Sanderson EW, Valladares F, Vilà M, Zamora R & Zobel M (2006) Novel ecosystems: Theoretical and management aspects of the new ecological world order. *Global Ecology and Biogeography* 15: 1–7. doi:10.1111/j.1466-822X.2006.00212.x.
- Jędrzejewska B & Jędrzejewski W (1998) Predation in vertebrate communities: The Białowieża Primeval Forest as a case study. Springer Science & Business Media.

- Kauhala K & Kowalczyk R (2011) Invasion of the raccoon dog *Nyctereutes procyonoides* in Europe: History of colonization, features behind its success, and threats to native fauna. *Current Zoology* 57: 584–598. doi:10.1093/czoolo/57.5.584.
- Kauhala K, Laukkanen P & von Rége I (1998) Summer food composition and food niche overlap of the raccoon dog, red fox and badger in Finland. *Ecography* 21: 457–463. doi:10.1111/j.1600-0587.1998.tb00436.x.
- Kochmann J, Cunze S & Klimpel S (2021) Climatic niche comparison of raccoons *Procyon lotor* and raccoon dogs *Nyctereutes procyonoides* in their native and non-native ranges. *Mammal Review* 51: 585–595. doi:10.1111/mam.12249.
- Kowalczyk R, Jędrzejewska B, Zalewski A & Jędrzejewski W (2008) Facilitative interactions between the Eurasian badger (*Meles meles*), the red fox (*Vulpes vulpes*), and the invasive raccoon dog (*Nyctereutes procyonoides*) in Białowieża Primeval Forest, Poland. *Canadian Journal of Zoology* 86: 1389–1396. doi:10.1139/Z08-127.
- Kowalczyk R, Zalewski A, Jędrzejewska B & Jędrzejewski W (2003) Spatial organization and demography of badgers (*Meles meles*) in Białowieża Primeval Forest, Poland, and the influence of earthworms on badger densities in Europe. *Canadian Journal of Zoology* 81: 74–87. doi:10.1139/z02-233.
- Kowarik I (1995) Time lags in biological invasions with regard to the success and failure of alien species: Plant invasions: general aspects and special problems (ed. by P Pyšek, K Prach, M Rejmánek & M Wade) SPB Academic Publishing, pp. 15–38.
- Kuebbing SE (2020) How direct and indirect non-native interactions can promote plant invasions, lead to invasional meltdown and inform management decisions: Plant invasions: The role of biotic interactions (ed. by A Traveset & DM Richardson), pp. 153–176. doi:10.1079/9781789242171.0153.
- Kurek P (2015) Consumption of fleshy fruit: Are central European carnivores really less frugivorous than southern European carnivores? *Mammalian Biology* 80: 527–534. doi:10.1016/j.mambio.2015.10.001.
- 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. doi:10.3897/neobiota.93.128008.
- Labbé MA & King DI (2020) Songbird Use of Native and Invasive Fruit in the Northeastern USA. *Wildlife Society Bulletin* 44: 570–578. doi:10.1002/wsb.1113.
- Latham ADM, Warburton B, Byrom AE & Pech RP (2017) The ecology and management of mammal invasions in forests. *Biological Invasions* 19: 3121–3139. doi:10.1007/s10530-017-1421-5.
- Laurimaa L, Süld K, Davison J, Moks E, Valdmann H & Saarma U (2016) Alien species and their zoonotic parasites in native and introduced ranges: The raccoon dog example. *Veterinary Parasitology* 219: 24–33. doi:10.1016/j.vetpar.2016.01.020.
- López-Darias M & Nogales M (2008) Effects of the invasive Barbary ground squirrel (*Atlantoxerus getulus*) on seed dispersal systems of insular xeric environments. *Journal of Arid Environments* 72: 926–939. doi:10.1016/j.jaridenv.2007.12.006.
- Łubek A, Adamowski W, Dyderski MK, Wierzchołska S & Czortek P (2025) Invasive *Prunus cerasifera* Ehrh. Hosts more lichens than native tree species – does quantity reflect quality? *Forest Ecology and Management* 590: 122812. doi:10.1016/j.foreco.2025.122812.
- Majewski K, Gris VN, Miyabe-Nishiwaki T & MacIntosh AJ (2026) Mesocarnivore on the move: an updated review on the spread and ecological effects of invasive *Nyctereutes procyonoides*. *Biological Invasions* 28: 83. doi:10.1007/s10530-026-03776-9.
- Martin PH, Canham CD & Marks PL (2009) Why forests appear resistant to exotic plant invasions: Intentional introductions, stand dynamics, and the role of shade tolerance. *Frontiers in Ecology and the Environment* 7: 142–149. doi:10.1890/070096.
- Meek PD, Ballard G, Claridge A, Kays R, Moseby K, O'Brien T, O'Connell A, Sanderson J, Swann DE, Tobler M & Townsend S (2014) Recommended guiding principles for reporting on camera trapping research. *Biodiversity and Conservation* 23: 2321–2343. doi:10.1007/s10531-014-0712-8.
- Mitchell MS & Powell RA (2004) A mechanistic home range model for optimal use of spatially distributed resources. *Ecological Modelling* 177: 209–232. doi:10.1016/j.ecolmodel.2004.01.015.
- Mulder JL (2012) A review of the ecology of the raccoon dog (*Nyctereutes procyonoides*) in Europe. *Lutra* 55: 101–127.
- Nowak E & Pielowski Z (1964) Distribution of the raccoon dog in Poland related to its immigration and spread in Europe. *Acta Theriologica* 9: 81–110.
- Nowakowski K, Ważna A, Kurek P, Cichocki J & Gabryś G (2020) Reproduction success in European badgers, red foxes and raccoon dogs in relation to sett cohabitation. *PLOS ONE* 15: e0237642. doi:10.1371/journal.pone.0237642.
- Padrón B, Nogales M, Traveset A, Vilà M, Martínez-Abraín A, Padilla DP & Marrero P (2011) Integration of invasive *Opuntia* spp. By native and alien seed dispersers in the Mediterranean area

- and the Canary Islands. *Biological Invasions* 13: 831–844. doi:10.1007/s10530-010-9872-y.
- Pagh S, de Jonge N, Østergaard SK, Pertoldi C, Woolbridge B, Laustsen AM, Svenning J-C, Pedersen MF, Larsen HL, Nielsen JL & Toft S (2025) Diet of raccoon dogs (*Nyctereutes procyonoides*) in Danish wetlands with focus on ground-nesting birds and amphibians. *European Journal of Wildlife Research* 71: 14. doi:10.1007/s10344-024-01886-0.
- Pigozzi G (1992) Frugivory and seed dispersal by the European badger in a Mediterranean habitat. *Journal of Mammalogy* 73: 630–639. doi:10.2307/1382035.
- Pyšek P, Hulme PE, Simberloff D, Bacher S, Blackburn TM, Carlton JT, Dawson W, Essl F, Foxcroft LC, Genovesi P, Jeschke JM, Kühn I, Liebhold AM, Mandrak NE, Meyerson LA, Pauchard A, Pergl J, Roy HE, Seebens H, van Kleunen M, Vilà M, Wingfield MJ & Richardson DM (2020) Scientists' warning on invasive alien species. *Biological Reviews* 95:1511–1534. doi:10.1111/brv.12627.
- R Core Team (2025) R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. version 4.3.0 "Already Tomorrow". <http://www.R-project.org/>.
- Saracco JE, Collazo JA & Groom MJ (2004) How do frugivores track resources? Insights from spatial analyses of bird foraging in a tropical forest. *Oecologia* 139: 235–245. doi:10.1007/s00442-004-1493-7.
- Seebens H, Blackburn TM, Dyer EE, Genovesi P, Hulme PE, Jeschke JM, Pagad S, Pyšek P, Winter M, Arianoutsou M, Bacher S, Blasius B, Brundu G, Capinha C, Celesti-Grapow L, Dawson W, Dullinger S, Fuentes N, Jäger H, Kartesz J, Kenis M, Kreft H, Kühn I, Lenzner B, Liebhold A, Mosena A, Moser D, Nishino M, Pearman D, Pergl J, Rabitsch W, Rojas-Sandoval J, Roques A, Rorke S, Rossinelli S, Roy HE, Scalera R, Schindler S, Štajerová K, Tokarska-Guzik B, van Kleunen M, Walker K, Weigelt P, Yamanaka T & Essl F (2017) No saturation in the accumulation of alien species worldwide. *Nature Communications* 8: 14435. doi:10.1038/ncomms14435.
- Shiels AB & Drake DR (2011) Are introduced rats (*Rattus rattus*) both seed predators and dispersers in Hawaii? *Biological Invasions* 13: 883–894. doi:10.1007/s10530-010-9876-7.
- Sidorovich VE, Polozov A, Lauzhel G & Krasko D (2000) Dietary overlap among generalist carnivores in relation to the impact of the introduced raccoon dog *Nyctereutes procyonoides* on native predators in northern Belarus. *Zeitschrift für Säugetierkunde* 65: 271–285.
- Sidorovich VE, Solovej IA, Sidorovich AA & Dyman AA (2008) Seasonal and annual variation in the diet of the raccoon dog *Nyctereutes procyonoides* in northern Belarus: The role of habitat type and family group. *Acta Theriologica* 53: 27–38. doi:10.1007/BF03194276.
- Simberloff D, Relva MA & Nuñez M (2002) Gringos En El Bosque: Introduced Tree Invasion in a Native *Nothofagus/Austrocedrus* Forest. *Biological Invasions* 4: 35–53. doi:10.1023/A:1020576408884.
- Simberloff D & Von Holle B (1999) Positive interactions of nonindigenous species: Invasional meltdown? *Biological Invasions* 1: 21–32. doi:10.1023/A:1010086329619.
- Smirnov NS (1965) Ekzoty Belovežskoj Pušči i ejookresnostej. Mscr.
- Sol D, González-Lagos C, Moreira D, Maspons J & Lapedra O (2014) Urbanisation tolerance and the loss of avian diversity. *Ecology Letters* 17: 942–950. doi:10.1111/ele.12297.
- Sutor A (2008) Dispersal of the alien raccoon dog *Nyctereutes procyonoides* in Southern Brandenburg, Germany. *European Journal of Wildlife Research* 54: 321–326. doi:10.1007/s10344-007-0153-8.
- Sutor A, Kauhala K & Ansorge H (2010) Diet of the raccoon dog *Nyctereutes procyonoides* – A canid with an opportunistic foraging strategy. *Acta Theriologica* 55: 165–176. doi:10.4098/j.at.0001-7051.035.2009.
- Takatsuki S, Miyaoka R & Sugaya K (2018) A comparison of food habits between Japanese marten and raccoon dog in Western Tokyo with reference to fruit use. *Zoological Science* 35: 68–74. doi:10.2108/zs170116.
- Tedeschi L, Biancolini D, Capinha C, Rondinini C & Essl F (2022) Introduction, spread, and impacts of invasive alien mammal species in Europe. *Mammal Review* 52: 252–266. doi:10.1111/mam.12277.
- Tedeschi L, Lenzner B, Schertler A, Wessely J, Biancolini D, Capinha C, Melone B, Diana Soria C, Rondinini C & Essl F (2025) Patterns and drivers of range filling of alien mammals in Europe. *Oikos* 2025: e11388. doi:10.1002/oik.11388.
- Traveset A & Richardson DM (2014) Mutualistic interactions and biological invasions. *Annual Review of Ecology, Evolution and Systematics* 45: 89–113. doi:10.1146/annurev-ecolsys-120213-091857.
- Vergara-Tabares DL, Badini J & Peluc SI (2015) Fruiting phenology as a “triggering attribute” of invasion process: Do invasive species take advantage of seed dispersal service provided by native birds? *Biological Invasions* 18: 677–687. doi:10.1007/s10530-015-1039-4.
- Wasserstein RL & Lazar NA (2016) The ASA's statement on p-Values: context, process, and purpose. *American Statistician* 70: 129–133. doi:10.1080/00031305.2016.1154108.
- Wereszczuk A & Zalewski A (2015) Spatial niche segregation of sympatric stone marten and pine

- marten – avoidance of competition or selection of optimal habitat? PLoS ONE 10: e0139852. doi:10.1371/journal.pone.0139852.
- 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. doi:10.3897/neobiota.81.95849.
- Wooldridge B, Svenning J-C & Pugh S (2024) Habitat selection and movement patterns of the Raccoon dog (*Nyctereutes procyonoides*) in Denmark using GPS telemetry data. *European Journal of Wildlife Research* 70: 64. doi:10.1007/s10344-024-01803-5.
- Wright TF, Eberhard JR, Hobson EA, Avery ML & Russello MA (2010) Behavioral flexibility and species invasions: The adaptive flexibility hypothesis. *Ethology Ecology & Evolution* 22: 393–404. doi:10.1080/03949370.2010.505580.
- Zalewski A (2005) Geographical and seasonal variation in food habits and prey size of European pine martens: Martens and fishers (*Martes*) in human-altered environments (ed. by DJ Harrison, AK Fuller & G Proulx) Springer-Verlag, pp. 77–98. doi:10.1007/0-387-22691-5\_3.