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Climate warming, ecological dynamics and nature conservation drive tree diversity in Wigierski National Park, Poland

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Abstract: In response to ongoing climate warming, tree species adapted to colder climates are expected to shift their geographic ranges northward. Within the framework of long-term ecological monitoring in Wigry National Park (northeastern Poland), observed changes in forest biocenoses reflect the combined influence of climate change and natural ecological dynamics.

This study compares dendroflora composition and diversity between two monitoring periods, 2011 and 2024, as part of an ongoing effort to track climate-related ecological shifts. Tree observations and measurements were carried out using concentric circular plots. In the largest plots, all trees with a diameter at breast height (d.b.h.) $\geq$ 12 cm were recorded by species, and their d.b.h. was measured. In the smaller plots, all trees with a d.b.h. $\geq$ 2 cm and $<$ 2 cm but taller than 30 cm were similarly identified and measured. Data were recorded with Field-Map software integrated with an electronic calliper. The species-level taxonomic data, individual counts and basal area per species and plot were used to calculate biodiversity indices.

Over the 13-year interval, a marked increase in overall dendroflora diversity was observed. Notably, the dominance of canopy-forming conifers – *Pinus sylvestris* and, to a lesser extent, *Picea abies* – measured as the proportion of individuals or stem density, has declined. This decline of coniferous species has been accompanied by an increase in the abundance and diversity of broadleaved deciduous species, including *Tilia cordata*, *Quercus robur*, *Betula pendula*, and *Acer platanoides*. Other thermophilous deciduous taxa also exhibited upward trends in both presence and abundance. Furthermore, the exponential of Shannon entropy, reached the highest value when evergreen conifers comprised 35% of the stand composition in 2011 and 18% in 2024.

This finding suggests that maximum dendroflora diversity reaches its highest level at an intermediate proportion of conifers presence, rather than under conifers dominance or absence. Collectively, the processes occurring in Wigierski National Park illustrate the gradual shift in ecotonal forest ecosystems from cold-adapted coniferous species to broadleaved deciduous taxa due to ongoing climate change.

Keywords: biodiversity, climate change, forest conservation, forest ecosystem, trees

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Introduction

Mean annual air temperatures are projected to rise by more than 1.5 °C over the 21st century. As global temperatures continue to increase, all regions are expected to experience increasingly frequent and concurrent changes in climate impact-drivers. Extreme weather events like simultaneous heatwaves and droughts are anticipated to become more common, often occurring at the same time across multiple regions (IPCC 2023). However, natural variability driven by the inherently chaotic nature of the climate system, plays a significant role at local spatial scales and across seasonal to decadal periods (Hawkins & Sutton, 2012).

In northern and western Europe, rising atmospheric CO_2 concentrations and higher temperatures are generally expected to boost forest growth and timber production in the short to medium term. However, these benefits may be outweighed by increasing risks of drought and disturbances, particularly in southern and eastern Europe (Lindner et al., 2010). The effects of increased CO_2 concentrations on photosynthesis and tree growth, as observed under semi-natural experimental conditions in forests (e.g. in open-top chambers or at the Swiss Canopy Crane site), have not always aligned with expectations. Results from a long-term study on the responses of ten tree species to elevated CO_2 concentrations indicate that the indirect effects of CO_2 on the nitrogen cycle and water use may be more significant than the anticipated fertilization effect (Bader et al., 2013). In the ecotone between temperate and boreal zones in North America, warming experiments have shown that tree species native to more northerly ranges exhibit lower photosynthetic temperature optima and slower growth rates compared to species originating from more southern ranges (Sendall et al., 2015).

Consequently, the natural geographical ranges of economically important evergreen conifers in North America and Europe are projected to shift northward, with range contractions at their southern boundaries. This pattern has been observed in *Pinus sylvestris* L. (Reich & Oleksyn, 2008). Simultaneously, thermophilic deciduous broadleaved species are expanding into newly available niches, thereby increasing their distribution ranges (Lindner et al., 2010). These projections, based on bioclimatic models (Dyderski et al., 2025) and, in some cases, genomic studies (Milesi et al., 2018) are further supported by experimental research investigating tree responses to warming (Reich et al., 2015, 2016). With continued warming, broadleaved deciduous species may expand into boreal forests, increasing both species and functional diversity (Thuiller et al., 2006; Reich et al., 2015). In western and central Europe, conifers may increasingly be replaced by more heat-tolerant and competitive deciduous species (Lindner et al., 2010). These findings suggest that boreal species may retreat northward while temperate species expand into the ecotone increasing their ranges not only at global but also across small spatial scale, as population-level responses in growth and physiology may deviate from these global patterns due to local adaptation, genetic drift, phenotypic plasticity, and fitness differences (e.g, Gougherty et al., 2021). For example, in the Carpathian Mountains, *Abies alba* Mill. and *Fagus sylvatica* L. exhibited upslope expansion in Babiogórski National Park, whereas no such pattern was observed in the nearby Gorczański National Park, despite similar altitudinal temperature gradients (Gazda et al., 2019). However, long-term datasets linking meteorological variables with species composition and tree growth responses remain scarce, especially that verification is needed to determine whether plant species can be classified as expanding “winners", declining “losers", or those with uncertain outcomes at the local scales (Dyderski et al., 2018).

Changes in the species composition of Polish forests were recorded on study plots established by Włoczewski in Białowieża National Park in 1936 (Kowalski, 1994). This long-term study in the Białowieża Forest has been continued, providing unique datasets on changes in the composition and structure of dendroflora in a strictly protected Central European forest (Bernadzki et al., 1998; Brzeziecki, 2017).

In unmanaged forests, changes in tree species composition and stand structure are driven by a combination of climatic conditions, soil properties, topography, canopy dominance, species-specific adaptability, and phenotypic plasticity (Svenning & Skov, 2005; Turcotte & Levine, 2016). In managed forests, anthropogenic influences play a dominant role, interacting with environmental factors to shape species composition and stand dynamics. In contrast, strict nature reserves and national parks allow for the observation of natural successional processes with minimal human interference. These areas are particularly valuable for distinguishing the effects of climate change from those of forest management. Over the long term, protected areas serve as natural laboratories for monitoring ecosystem responses, and in the short term, they provide insights into species fluctuations attributable to global climate change. These sites often function as biodiversity hotspots, harbouring rare and endangered species (Myers et al., 2000). Long-term monitoring in protected areas can provide valuable empirical support for the bioclimatic forecasts. Although local changes in plant communities may reflect global trends, plant responses to climate warming at specific sites can diverge due to factors such as local ecotypic adaptation, genetic drift, migration, hybridization, and other evolutionary processes (Robakowski et al., 2012; Oddou-Muratorio et al., 2020; Heuertz et al., 2023).

This study was conducted in Wigry National Park (WNP), located in northeastern Poland. Prior to the park's designation, the dominant tree species were *Pinus sylvestris* L., *Picea abies* (L.) H. Karst., and a limited number of naturally regenerating or planted broadleaved species. In the 1980s and 1990s, a decline in *Picea abies* and *Pinus sylvestris* was observed, likely due to stand age and drought. In *P. abies*, increased frequency and intensity of *Ips typographus* L. outbreaks significantly contributed to higher mortality rates (Łoziński, 2002; Conservation Plan of Wigry National Park 2016). In 2020, the volume of beetle-infested deadwood in WNP was 3,009 m^3, which was considered a stable and secure level (Analysis of Wigry National Park's Activities 2023). This dieback was accompanied by both natural and artificial regeneration of *P. abies* and an increasing presence of broadleaved tree species. As a protected area, WNP serves not only as a biodiversity hotspot, but also as a valuable site for monitoring natural successional processes and forest responses to climate change.

The primary aim of this study was to compare tree species composition, the abundance of individuals per species, and tree species diversity indices in WNP thirteen years after an initial inventory. We tested the following hypotheses: (1) Tree diversity in WNP has increased, as indicated by diversity indices, and this increase is associated with a decline in the proportion of evergreen conifers. (2) The observed changes in species composition reflect a broader trend toward a higher proportion of warm-tolerant, drought-resistant deciduous species. An alternative hypothesis proposes that these local changes are independent of climate warming and do not align with global projections.

Study area

History, geographical conditions and forest communities

The oldest source of information on land use in our study area is the Map of Lake Wigry and the Suwałki region (1855), archived at the Lithuanian State Historical Archive, Vilnius, Lithuania (Fig. 1a). This map shows that 170 years ago, 72 of our 75 plots were forested. Only three plots are located in an area for which two map sheet are missing (grey area). However, we have a cartographer's sketch indicating that this area was classified as forest. Our study area has not been subject to intensive agricultural or industrial activity. However, on boreal sites in particular, *P. sylvestris* was planted following clear-cutting. The most intensive logging occurred during the First World War. In the 1930s, forest exploitation generally became less intensive, and the first conservation measures were introduced (Bogusławski, 2003).

In Wigry National Park, active conservation practices, such as occasional selective cutting and stand transformation, have been implemented (Conservation Plan of Wigry National Park, 2016; Analysis of Wigry National Park's Activities, 2021). On two of our 75 monitoring plots, active measures have been observed, including the removal of individual trees and partial cutting to support stand transformation.

Wigry National Park was established in 1989. It is located in the north easternmost part of Poland, near the Polish-Lithuanian border, between 53°57' and 54°10' N latitude, and between 22°57' and 23°15' E longitude. The northern section of the park lies within the eastern Suwałki Lake District, while the southern section is part of the Augustów Plain. The park covers an area of 151.13 km^2. It contains 42 lakes, the largest of which is Lake Wigry, covering 21.18 km^2 and reaching a depth of 73 meters. The terrain is hilly, with relative elevations varying by tens of meters; the highest point rises to 171.5 meters above sea level. The area is covered by glacial sediments from the Vistulian Glaciation, up to 150 meters thick. Soils developed from this allochthonous material include rusty soils (arenosols) and podzolic soils (Migaszewski et al., 2004).

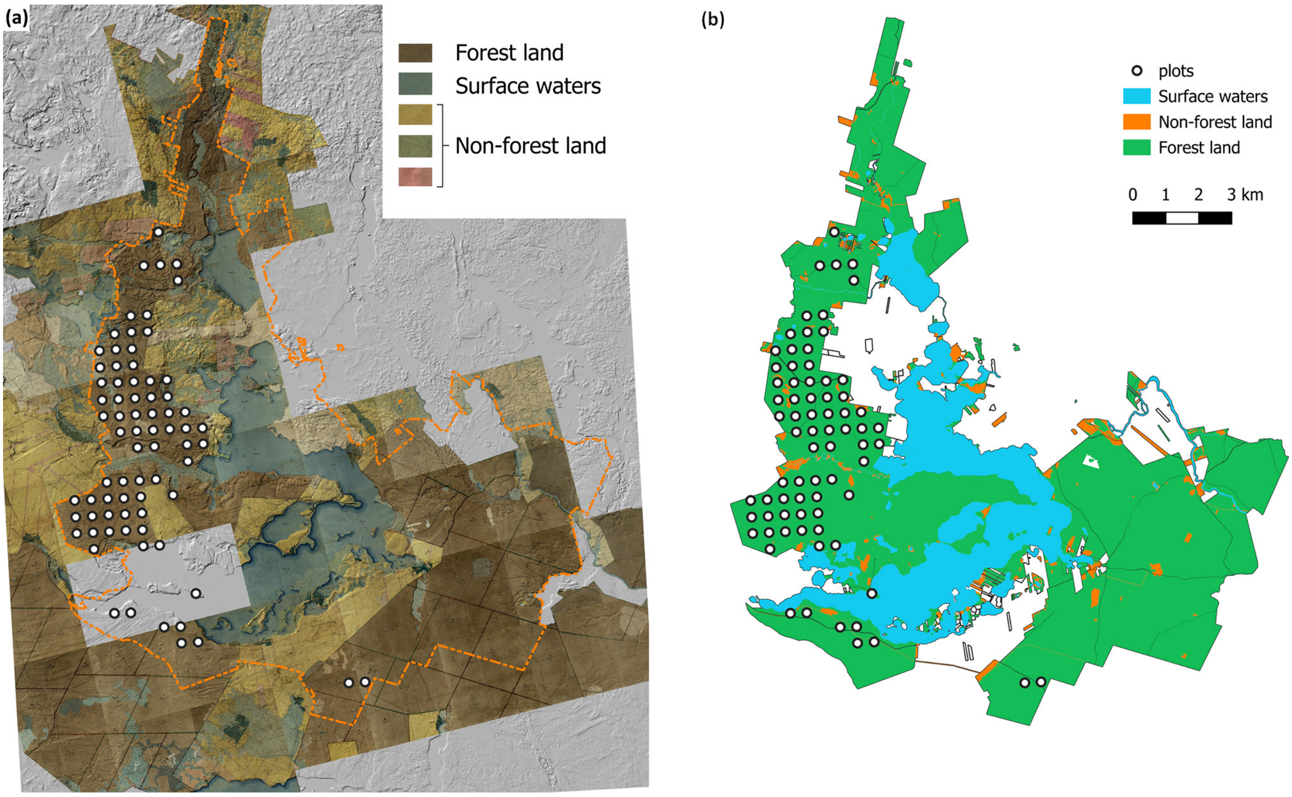

Fig. 1. a. Map of the Lake Wigry region from 1855, showing the plots surveyed in 2024. Grey – no data; orange line – current boundary of Wigierski National Park; white points – monitoring plots. Published with permission of the Lithuanian State Historical Archive; b. Map of Wigierski National Park showing monitoring plots inventoried in 2011 and 2024

The dominant forest community in WNP are the subboreal mixed coniferous forest (*Serratulo-Pinetum* J.MAT.1981) and the subcontinental oak–hornbeam forest (*Tilio cordatae–Carpinetum betuli* Tracz 1962), which occurs on eutrophic sites and supports a rich diversity of forest flora (Sokołowski, 1980, 1988). This includes protected plant species such as *Daphne mezereum*, *Lilium martagon*, and *Aquilegia vulgaris*. The oak–hornbeam forests are also notable for their high diversity of lichens, mosses, and fungi (Matuszkiewicz, 2001; Danielewicz & Pawlaczyk, 2004). According to the Map of Potential Natural Vegetation, our study plots are located within subboreal rich or poor *Tilio-Carpinetum* communities (Matuszkiewicz & Wolski, 2023).

Climate

Climatic data from the Suwałki meteorological station (latitude: 54°07'51", longitude: 22°56'56") confirm that local air temperature increases are consistent with global warming trends. A comparison of mean monthly temperatures between 1931–1980, and 1981–2019 reveals an increase of about 2 °C in January and February. Temperature increases were recorded in every month of the year (Górniak, 2021). The thermal distinctiveness of the Suwałki Lakeland has diminished, as evidenced by the positive mean March temperatures (Kejna & Rudzki, 2021). In recent decades, the total annual precipitation has not changed significantly but has fluctuated considerably, ranging from 450 to 800 mm. Snow cover periods have shortened, and snowfall has become less frequent and less intense. Importantly for vegetation, the duration of sunshine has increased. Meteorological observations in Suwałki confirm the phenomenon of global brightening. Although total precipitation has remained relatively stable, drought events have become twice as frequent when comparing the periods 1961–1987 and 1988–2019. This suggests that droughts are primarily driven by rising temperatures and increased evapotranspiration rates, with periodic reductions in precipitation playing a secondary role. In the Suwałki Lakeland, including Wigry National Park, the growing season has been extended by approximately 2 to 3 weeks (Górniak, 2021).

Materials and Methods

Materials

The study trees represented three functional groups: (1) evergreen conifers: *Picea abies* Karst. and *Pinus sylvestris* L.; (2) deciduous conifers: *Larix decidua* Mill.; (3) deciduous broadleaved: *Betula pendula* Roth, *Betula pubescens* Ohrh., *Prunus* (mainly *Prunus padus* L.), *Quercus rubra* L., *Quercus robur* L., *Carpinus betulus* L., *Salix caprea* L., *Malus sylvestris* L. (Mill.), *Sorbus aucuparia* L., *Fraxinus excelsior* L., *Acer pseudoplatanus* L., *Acer platanoides* L., *Tilia cordata* Mill., *Alnus glutinosa* (L.) Gaertn., *Populus tremula* L. These species were further categorized based on successional status. Pioneer species include: *P. sylvestris*, *L. decidua*, *B. pendula*, *Salix*, *P. tremula*. Late-successional (climax) species include *T. cordata*, *C. betulus*, *A. glutinosa*, *Q. robur* and *rubra*. Both *Acer* sp., *P. padus*, and *M. sylvestris*, *S. aucuparia* are considered intermediate in successional status. *Picea abies* demonstrates both pioneer and climax characteristics, as it is capable of regenerating under canopy cover as well as in large gaps. Pioneer species are generally shade-intolerant. Among the deciduous broadleaved trees, most are shade-tolerant, with the exception of *Q. robur*, *F. excelsior* and *B. pubescens*, which are shade-tolerant only in their juvenile stages (Grime, 1977; Brzeziecki & Kienast, 1994). *Pinus sylvestris* and *P. abies* exhibit high ecological plasticity and are well-adapted to cold climates, with the majority of their geographical ranges located within the boreal zone. *Picea abies* and *L. decidua* are generally more sensitive to drought compared to *P. sylvestris*. Sokołowski (1980) observed that in north-eastern Poland, including Wigry National Park, *P. abies* is a natural component of *Tilio-Carpinetum*. Broadleaved deciduous species such as *T. cordata*, *A. pseudoplatanus*, and *A. platanoides* need higher temperatures and probably possess higher values of optimal temperatures for photosynthesis compared with boreal tree species (Zarzycki et al., 2002; Kumarathunge et al., 2019).

Methods

Monitoring network for dendroflora diversity in Wigry National Park

In 2011, a monitoring network consisting of 365 permanent plots in the regular gird of 0.5 km was established in WNP. The plots are representative of forest stands across various site types. In this study, 75 plots were selected to compare dendroflora diversity based on monitoring conducted twice on the same plots in 2011 and 2024. All plots are located in stands classified in 2011 as the *Tilio cordatae-Carpinetum betuli* forest community and were chosen as representative of this vegetation type. *Tilio-Carpinetum* was selected based on (1) its substantial current representation, covering 37% of the total forest area in WNP; (2) its high potential tree species diversity, which includes both boreal species such as *P. abies* and *P. sylvestris* and thermophilic deciduous species; and (3) information indicating increasing mortality of *P. sylvestris* and *P. abies* (Conservation Plan of Wigry National Park, 2016; personal communication). Tree observations and measurements were carried out using concentric circular plots. The largest circle had a radius of 12.61 m (500 m^2), within which all trees with a diameter at breast height (d.b.h.) ≥ 12 cm were recorded by species, and their d.b.h. were measured. In a smaller circle with a radius of 3.99 m (50 m^2), all trees with d.b.h. larger or equal to 2 cm were counted and measured similarly. In circle with a radius of 2.52 m (20 m^2), the height of seedlings higher or equal 30 cm and d.b.h. < 2 cm was measured.

In both 2011 and 2024, all tree species present on each of the 75 plots were identified, and the number of individuals per species was recorded. In 2011, d.b.h. was measured using a calliper with 1 mm precision. In 2024 data were recorded on a tablet equipped with Field-Map software (https://www.fieldmap.cz), integrated with an electronic calliper (MD II+, Haglöf Sweden AB) and laser rangefinder with compass (TruPulse 360B, Laser Technology Inc.). For this study, we used species-level taxonomic data and individual counts per species and plot to calculate biodiversity indices.

Calculation and interpretation of selected diversity indices

Three commonly used biodiversity indices: exponential Shannon entropy (^1D – the Hill number of order 1), inverse Simpson index (^2D – the Hill number of order 2), and Margalef index (*MRI*) were used to compare diversity of the dendroflora in the monitoring plots of WNP (Jost, 2006; Kumar et al., 2022). The Shannon diversity index takes into account both richness (number of species) and evenness (distribution of individuals among species) (Shannon, 1948).

$$H' = \sum_{n-1}^{S} p_i ln p_i \tag{1}$$

$$p_i = \frac{n_i}{N} \tag{2}$$

where: p_i – proportion of individuals belonging to species i, S – total number of species (species richness), ln – natural logarithm, n_i – number of individuals of species i, N – total number of individuals in the sample.

A higher value of H' indicates higher diversity, and a lower value points out lower diversity.

$$^1D = e^{H'} \tag{3}$$

where: ^1D – exponential Shannon entropy, e – base of the natural logarithm.

The exponential Shannon entropy informs on the number of equally abundant species that would produce the same Shannon entropy as the observed community (Jost, 2006; Chao et al., 2014).

The Simpson index (D) calculates the probability how likely the randomly selected individuals are not from the same species. Its value increases with decreasing biodiversity. The inverse Simpson index (^2D – the effective number of dominant species or the Hill number of order 2) increases with increasing biodiversity.

$$^{2}D = \frac{1}{H' = \sum_{i=1}^{S} p_i^2} \tag{4}$$

where: S – total number of species (species richness), p_{i} – proportion of individuals belonging to species i, calculated with equation 2. The high value of ^2D means high diversity and an equilibrium of number of individuals among the species. The low value of ^2D can be interpreted as dominance of one species (Hill, 1973; Chao et al., 2014).

The Margalef index is used to measure the species richness relative to the sample size and cannot be recalculated to become the Hill number (Margalef, 1958).

$$MRI = \frac{S - 1}{\ln (N)} \tag{5}$$

The high values of *MRI* indicate the high diversity of species relative to the number of individuals. The lower values inform that a low number of species dominates in the given site.

Statistical analyses

The meteorological data was acquired from the Institute of Meteorology and Water Management public database (https://danepubliczne.imgw.pl/). Mean daily temperature and sum of daily precipitation data for the nearest meteorological station Suwałki (22°56'56"; 54°07'51") was used to calculate mean annual temperature (MAT, °C) and total annual precipitation (TAP, mm). The number of days with snow cover was summarised for each cold season. We assumed that the vegetative season starts after a five-day period with the mean daily minimum temperature above 5 °C, and ends after a five-day period with the mean daily maximum temperature below 5 °C.

The values of the diversity indices were calculated using the data collected on 75 plots in 2011 and 2014, separately. The exponential Shannon entropy, effective number of dominant species, and Margalef indices were calculated for each plot in *R* (R Core Team 2025) using the package *vegan* (Oksanen et al., 2025). The values of indices were modelled using linear mixed model with one independent fixed factor – time of inventory (categorical with two levels: 2011 or 2024). We used plot as random intercept to incorporate the dependency among observations. The model was tested for normality and homoscedasticity of residuals. The linear mixed models were fitted using the function *lmer* in package *lme4* (Bates et al., 2015). The value of marginal coefficient of determination (R^2) was calculated to estimate the variance explained by the fixed effect of year, and the value of conditional R^2 for the effect of year and the random effect of the plot. For checking assumptions, the package *performance* was used (Lüdecke et al., 2021).

The relationship between the proportion of conifers and indices of diversity values was fitted with the parabolic model:

$$y = ax^2 + bx + c \tag{6}$$

The values of proportion of conifers (x) at the maximal value of each index was calculated from the equation:

$$x = \frac{-b}{2a} \tag{7}$$

Then, the maximal value of the index was calculated from equation (6).

Results

Climate fluctuations

From 1961 to 2024, the mean annual temperature increased by approximately 1.5 °C, while total annual precipitation varied widely from 450 to 800 mm without showing a significant long-term trend (Fig. 2). During this period, the highest recorded mean monthly temperature was 21.5 °C in July 2021, and sum of yearly precipitation ranged from 394 mm in 1968 to 856 mm in 2017. The number of days with snow cover decreased significantly by approximately 30 days, affecting water availability at the beginning of vegetation season (Fig. 3). Additionally, the vegetation period has extended by an average of two weeks (Fig. 4).

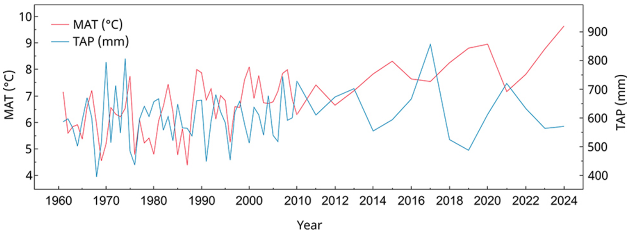

Fig. 2. Mean annual temperature and mean annual precipitation. The data are from the Suwałki Meteorological Station (longitude: 22°56'56"; latitude: 54°07'51"). The X-axis scale is changed after 2010 to emphasise the period studied. MAT – mean annual temperature; TAP – total annual precipitation

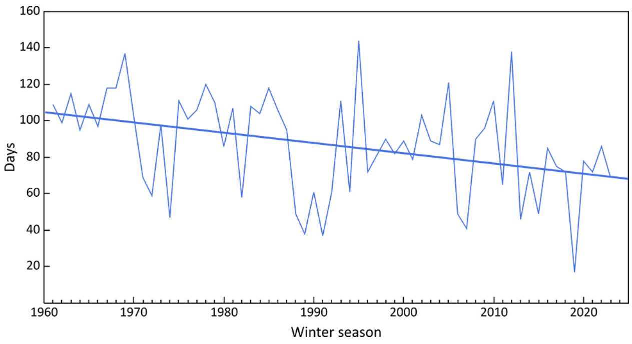

Fig. 3. Total number of days with snow cover. Data from the Suwałki Meteorological Station (22°56'56"; 54°07'51")

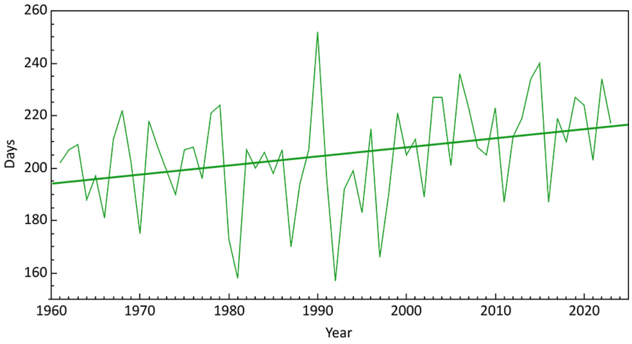

Fig. 4. The duration of the vegetative season. It was assumed that the growing season begins and ends when the minimum temperature remains above 5 °C for five days

Understory regeneration

Among tree species in the understory layer taller than 30 cm and with d.b.h. smaller than 2 cm no individuals of *P. sylvestris* were found. This is a significant finding, considering that this species accounted for approximately 30% of individuals in the ≥12 cm d.b.h. class (compare Table 1 and Table 3). The relative abundance of *A. campestre*, *A. platanoides*, *F. excelsior*, *P. abies*, and *Q. robur* declined for different reasons between 2011 and 2024. In 2011, *A. campestre* was represented by only a small number of individuals, which were absent in 2024 and in higher d.b.h. classes. At d.b.h. < 2 cm, the reduction in *A. platanoides* (from 75 in 2011 to 45 trees in 2024) and in *Q. robur* (from 71 to 17) was primarily attributed to self-thinning. For *A. platanoides*, both a decline in the number of young trees (Table 1) and progression of individuals into higher d.b.h. classes at d.b.h. ≥12 cm (from 11 to 37 individuals) were observed while the presence of *Q. robur* was stable (325 individuals with d.b.h. ≥ 12 cm in 2011 and 2024 (Table 3).

Remarkable increases in the proportion of *C. betulus* (from 5 to 46 trees), *T. cordata* (from 26 to 60), and *U. laevis* (from 6 to 15 trees) were recorded in the understory at d.b.h. < 2 cm (Tables 1). This increasing trend from 2011 to 2024 in number of trees was also observed at d.b.h. between 2 cm and 12 cm for *C. betulus* and *T. cordata* (Table 2). The increase in natural regeneration of *C. betulus* was followed by only a limited shift of small trees into larger diameter classes (compare Tables 1, 2, 3).

Table 1. Proportions of tree species taller than 30 cm with a diameter at breast height (d.b.h.) less than 2 cm, calculated as the ratio of the number of individuals of each species to the total number of individuals, recorded on monitoring plots in 2011 and 2024. The last column shows the differences in species proportions between 2024 and 2011. All observations for each species and year were pooled from 75 plots, each with a radius of 2.52 m (20 m^2)

Species	Proportion of species (%)		2024–2011
	2011	2024	
Acer campestre L.	0.61	–	−0.61
Acer platanoides L.	45.45	17.51	−27.94
Acer pseudoplatanus L.	–	0.39	0.39
Alnus glutinosa (L.) Gaertn.	–	0.78	0.78
Betula sp.	–	0.39	0.39
Carpinus betulus L.	3.03	17.90	14.87
Fraxinus excelsior L.	0.61	0.39	−0.22
Picea abies Karst.	7.27	5.06	−2.21
Populus tremula L.	0.61	2.33	1.73
Prunus	3.64	6.23	2.59
Quercus robur L.	12.12	6.61	−5.51
Salix caprea L.	–	1.17	1.17
Sorbus aucuparia L.	–	12.06	12.06
Tilia cordata Mill.	15.76	23.35	7.59
Ulmus laevis Pall.	3.64	5.84	2.20

Table 2. Proportions of tree species with a diameter at breast height (d.b.h.) between 2 cm and 12 cm, calculated either as the ratio of the number of individuals of each species to the total number of individuals, or as the ratio of the basal area of each species to the total basal area, recorded on monitoring plots in 2011 and 2024. All observations for each species and year were pooled from 75 plots, each with a radius of 3.99 m (50 m^2)

Species	Number of individuals (%)		Basal area (%)	
	2011	2024	2011	2024
Acer	5.18	9.30	4.03	5.84
Alnus glutinosa (L.) Gaertn.	3.11	0.00	3.88	0.00
Betula	1.55	0.00	1.65	0.00
Carpinus betulus L.	3.63	9.30	1.45	2.40
Fraxinus excelsior L.	1.04	0.00	1.61	0.70
Picea abies Karst.	31.09	32.56	41.78	44.25
Pinus sylvestris L.	1.04	1.16	2.37	2.48
Populus tremula L.	0.52	0.00	0.36	0.00
Pyrus communis	0.00	2.33	0.00	0.23
Quercus robur L.	36.79	19.77	31.72	25.88
Sorbus aucuparia L.	1.04	2.33	1.61	0.70
Tilia cordata Mill.	9.84	17.44	6.85	8.21
Ulmus laevis Pall.	5.18	5.81	3.02	10.36

Table 3. Proportions of tree species with a diameter at breast height (d.b.h.) ≥ 12 cm, calculated either as the ratio of the number of individuals of each species to the total number of individuals, or as the ratio of the basal area of each species to the total basal area, recorded on the monitoring plots in 2011 and 2024. All the observations per species and year were pooled from 75 plots with a radius of 12.61 m (500 m^2)

Species	Number of individuals (%)		Basal area (%)	
	2011	2024	2011	2024
Acer platanoides L.	0.46	1.71	0.26	0.83
Acer pseudoplatanus L.	–	0.05	–	0.01
Alnus glutinosa (L.) Gaertn.	0.84	0.88	0.70	0.84
Betula pendula Roth	2.53	3.05	2.74	2.79
Betula pubescens Ohrh.	0.04	0.09	0.04	0.23
Carpinus betulus L.	0.46	0.69	0.34	0.47
Fraxinus excelsior L.	–	0.14	–	0.05
Larix decidua Mill.	0.63	0.65	1.03	0.80
Malus sylvestris L. (Mill.)	0.42	0.05	0.02	0.02
Picea abies Karst.	43.91	42.16	33.80	34.07
Pinus sylvestris L.	34.54	29.73	48.64	45.57
Populus tremula L.	0.38	0.23	0.90	0.67
Prunus	0.04	0.05	0.02	0.02
Quercus robur L.	13.71	15.03	9.88	11.00
Quercus rubra L.	–	0.09	–	0.05
Salix	0.04	–	0.01	–
Salix caprea L.	0.46	0.05	0.41	0.01
Sorbus aucuparia L.	0.42	0.09	0.01	0.02
Tilia cordata Mill.	1.77	4.99	1.14	2.44
Ulmus laevis Pall.	0.13	0.28	0.07	0.15

Both the proportion of individuals and the total basal area indicate that in the 2 cm ≤ d.b.h. < 12 cm class, *P. abies* was a dominant species, alongside *Q. robur*, while the proportion of *P. sylvestris* remained low (Table 2).

Generally, warm-tolerant, deciduous broadleaved species continue to dominate the understory, with *Q. robur*, *T. cordata*, *C. betulus*, and *A. platanoides* being the most prevalent in the lower undergrowth layer (Table 1). In the upper undergrowth layer, *P. abies* holds a prominent position in terms of both individual counts and basal area (Table 2).

The second and dominant canopy layer

Among tree species with d.b.h. ≥ 12 cm, the evergreen conifers *P. sylvestris* and *P. abies* were dominant. *Picea abies* has a higher proportion of individuals but a lower proportion of basal area compared to *P. sylvestris*, which is the opposite of the pattern observed in the undergrowth. The proportion of the deciduous conifer *L. decidua* was minimal. Notably, *Q. robur*, *T. cordata*, and *B. pendula* also made up a significant portion of the species composition, regardless of the measurement year (Table 3).

In 2011, 17 species were recorded, with *Prunus* and *Salix* identified at the genus level. By 2024, at the d.b.h. ≥ 12 cm, the number of recorded species had increased to 19 compared with 2011. Only one *Salix* species, *S. caprea*, was identified. Importantly, three new species: *A. pseudoplatanus*, *F. excelsior*, and *Q. rubra* were observed in 2024, though each was represented by a small number of individuals. *Acer pseudoplatanus* and *F. excelsior* reached a d.b.h. of ≥ 12 cm in the period between the two measurement sets. *Quercus rubra* was recorded in the d.b.h. ≥ 12 cm class only in 2024, suggesting that this species may have been overlooked in the earlier 2011 inventory.

From 2011 to 2024, the combined proportion of the two dominant evergreen conifers (*P. abies* and *P. sylvestris*) declined by 6.7%, with *P. sylvestris* showing the more pronounced decrease. The proportion of *P. abies* basal area slightly increased, and *P. sylvestris* decreased. The number of *P. abies* trees decreased from 1041 to 912, and the number of *P. sylvestris* trees from 819 to 643. The proportion of *L. decidua* slightly increased over the same period, although the total number of individuals remained low (Table 3).

In contrast to the evergreen conifers, the proportion of nearly all deciduous broadleaved species increased, with the most notable rises observed for *T. cordata*, *Q. robur*, and *A. platanoides*. For other deciduous species, the increase in the proportion of individuals remained below 1.0%. Notably, the basal area proportion of *P. abies* showed only a slight increase, whereas the basal area of deciduous trees increased significantly (Table 3). Overall, fifteen deciduous broadleaved species expanded their presence, while only three species, including the genus *Salix* and *Salix caprea* experienced a decline.

In 2024, the total number of inventoried trees was 208 fewer than in 2011. This decrease was due to a reduction in the number of evergreen conifer trees in the smallest d.b.h. class, which was predominantly

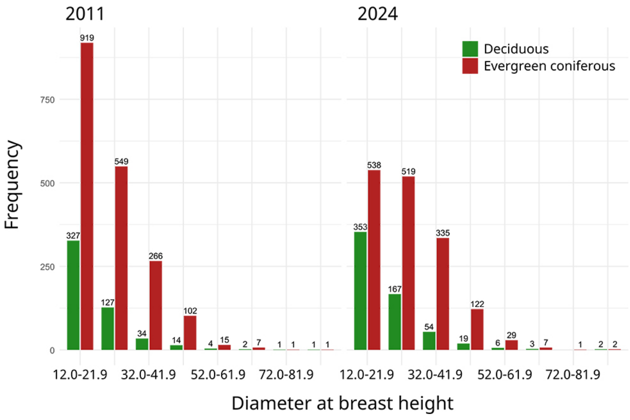

Fig. 5. The diameter at breast height (d.b.h.) structure of trees with d.b.h. ≥ 12 cm on monitoring plots in Wigierski National Park in 2011 and 2024 (n = 75, where n is the number of sampling units)

Table 4. Results of the linear mixed model for tree density (stems ha−¹) and basal area (m² ha−¹), presented separately for functional groups of tree species (deciduous and evergreen coniferous trees) in two inventory years (2011 and 2024). *SE* – standard error; CI – confidence interval; *LL* – lower limit of the confidence interval; *UL* – upper limit of the confidence interval (n = 75, where n is the number of sampling units)

Variable	Predictors	Estimate	SE	95% CI		*t*	*p*
				LL	UL		
Density (stems ha^{-1})	Intercept	284.3	15.5	253.8	314.8	18.3	<0.001
	Year (2024)	−53.8	20.2	−93.6	−14.1	−2.66	0.008
	Functional group (Deciduous)	−194.0	21.4	−236.0	−152.0	−9.08	<0.001
	2024 × Deciduous	57.9	29.2	0.46	115.3	1.98	0.048
Basal area (m^2 ha^{-1})	Intercept	28.02	1.41	25.25	30.80	19.9	<0.001
	Year (2024)	1.10	1.82	−2.49	4.68	0.60	0.55
	Functional group (Deciduous)	−20.14	1.94	−23.95	−16.34	−10.41	<0.001
	2024 × Deciduous	0.32	2.70	−4.98	5.63	0.12	0.91

occupied by *P. abies* (Fig. 5). Over the 13-year period, some *P. abies* individuals progressed into higher d.b.h. classes (Table 3, Fig. 5). In contrast, the number of deciduous trees increased across all d.b.h. classes between 2011 and 2024. The trends in tree species proportions shown in Table 3 were statistically confirmed for the two functional groups evergreen conifers and deciduous species in the linear mixed model (LMM) analysis (Table 4). Stem density (stems per ha) for trees with a diameter ≥ 12 cm, averaged across species grouped into the two functional types (deciduous and evergreen coniferous), decreased from 284 (±16) stems ha^{-1} in 2011 by 54 (±20) stems ha^{-1} by 2024. In 2011, the density of deciduous species was 194 (±21) stems ha^{-1} lower than that of evergreen coniferous species. However, over the 13-year period, the density of deciduous species increased by 58 (±29) stems ha^{-1} (Table 4).

Regarding basal area (m^2 ha^{-1}), the model estimated an average of 28.02 (±1.41) m^2 ha^{-1} across both functional groups. The increase in basal area over the 13 years 1.10 (±1.82) m^2 ha^{-1} was not statistically significant. Notably, evergreen coniferous species were dominant in terms of basal area: the average basal area of deciduous species was 20.14 (±1.94) m^2 ha^{-1} lower, and this difference remained unchanged after 13 years, with the interaction effect indicating an insignificant increase of only 0.32 (±2.70) m^2 ha^{-1} (Table 4).

Diversity of dendroflora

The values of ^1D, ^2D, and *MRI* indicate that overall dendroflora diversity in WNP was low to moderate. A significant increase in dendroflora diversity from 2011 to 2024 was detected regardless of whether the diversity indices were weighted by the number of individuals or by basal area (Tables 5 and 6). When weighted by the number of individuals, in 2024 ^1D increased by 0.215, ^2D by 0.034, and Margalef's index by 0.067 compared to their respective values of 2.450, 0.493, and 0.734 in 2011 (Table 5). When weighted by species basal area per hectare, ^1D and ^2D were 2.054 (±0.093) and 4.78 (±0.87), respectively (Table 6). In 2024, ^1D increased by 0.465, while ^2D decreased by 3 (Table 6). However, the fixed effect of year accounted for only a portion of the variance in the indices, as indicated by the marginal R^2 values. In contrast, a substantial proportion of variance was explained by the random effect of plot, reflected in the higher conditional R^2 values.

Positive differences in ^1D values between 2024 and 2011 were observed on 69% of the plots, indicating an increase in diversity (Fig. 6a). Only one plot showed no change ($^1D_{2024} - {}^1D_{2011} = 0$), while the remaining plots had negative values, indicating a decline. The inverse Simpson index increased on 67% of the plots ($^2D_{2024} - {}^2D_{2011} > 0$), suggesting an increase in diversity (Fig. 6b). For the Margalef index,

Table 5. Results of linear mixed model for exponentiated Shannon index (^1D – Hill number of order 1), inverse Simpson (^2D – Hill number of order 2) and Margalef biodiversity indices weighted by number of individuals in two inventories (2011 and 2024). SE – standard error; CI – confidence interval; LL – lower limit of the confidence interval; UL – upper limit of the confidence interval (n = 75, where n is the number of sampling units)

Index	Predictors	Estimate	SE	95% CI		*t*	*p*
				LL	UL		
^1D (individuals)	Intercept	2.450	0.094	2.262	2.637	25.97	<0.001
	Year (2024)	0.215	0.051	0.113	0.317	4.21	<0.001
^2D (individuals)	Intercept	0.493	0.018	0.458	0.528	27.94	<0.001
	Year (2024)	0.034	0.010	0.015	0.054	3.52	0.001
Margalef	Intercept	0.734	0.039	0.657	0.811	18.83	<0.001
	Year (2024)	0.067	0.021	0.025	0.108	3.15	0.002

Table 6. Results of linear mixed model for exponential Shannon entropy (^1D) and inverse Simpson (^2D) biodiversity indices weighted by basal area in two inventories (2011 and 2024). SE – standard error; CL – confidence interval; LL – lower limit of the confidence interval; UL – upper limit of the confidence interval (n = 75, where n is the number of sampling units)

Index	Predictors	Estimate	SE	95% CI		*t*	*p*
				LL	UL		
^1D (basal area)	Intercept	2.054	0.093	1.869	2.238	22.09	<0.001
	Year (2024)	0.465	0.089	0.287	0.642	5.21	<0.001
^2D (basal area)	Intercept	4.780	0.870	3.060	6.510	5.49	<0.001
	Year (2024)	−2.980	1.070	−5.090	−0.860	−2.78	0.006

72% of plots showed an increase ($MRI_{2024} - MRI_{2011} > 0$), 8% showed no change, and 20% showed a decrease (Fig. 6c).

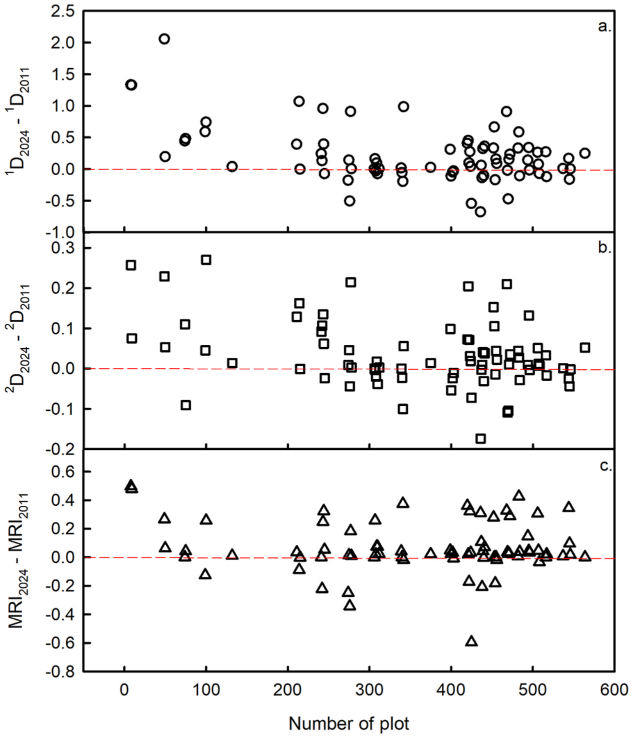

Fig. 6. Values representing the differences in diversity indices based on the number of individuals per tree species across 75 monitoring plots in Wigierski National Park. Each point shows the difference between the Hill numbers or Margalef index values recorded in 2024 and those recorded in 2011. a. Differences in the values of exponential Shannon index (^1D) ($^1D_{2024} - {}^1D_{2011}$); b. Differences in the values of inverse Simpson index ($^2D_{2024} - {}^2D_{2011}$); c. Differences in the values of Margalef index ($MRI_{2024} - MRI_{2011}$). The dashed red line corresponds to 0

Relations between the proportion of evergreen conifers and diversity indices

The relationships between the proportion of evergreen conifers (*P. sylvestris* and *P. abies*) and the values of diversity indices exhibit a parabolic pattern (Fig. 7). In this relationship, an autocorrelation exists because the proportion of conifers contributes directly to the calculation of each index. At lower proportions of conifers (left-hand side of the parabola), the diversity indices increase, reaching a maximum at the vertex of the parabolic curve. Beyond this point, the indices decline with further increases in conifer proportion. The curvature of the parabola reflects both the increasing proportion of deciduous broadleaved species and the decreasing proportion of conifers. Despite the presence of autocorrelation, this approach allows us to estimate the proportion of conifers at which each index reaches its maximum corresponding to the vertex of the respective parabola. These parabolic relationships are presented as an exploratory analysis to reveal potential non-linear patterns in species diversity along a gradient of conifer dominance. The vertex location serves as a descriptive benchmark rather than a causal threshold. The maximum value of ^1D, weighted by the number of individuals or basal area, was higher in 2024 at the lower conifer proportion as in 2011 (Table 7, Fig. 7a). This suggests that the increase in dendroflora diversity was driven by both a greater number of species and a more even distribution of individuals among non-coniferous tree species. Interestingly, the maximum value of ^1D weighted by tree basal area increased as the proportion of evergreen conifers decreased (Table 7, Fig. 7b). However, higher values of ^2D weighted by the number of individuals in 2024,

Table 7. The coordinates of the vertex of parabolic models applied to fit the relationship between the proportion of conifers and values of diversity indices (n = 75). The parabolic equations are shown in Fig. 7. ^1D (individuals or basal area) – exponential Shannon entropy calculated with the number of individuals or basal area at d.b.h; ^2D (individuals) – inverse Simpson index calculated with the number of individuals

Year	Index	Proportion of conifers	Index maximum
2011	^1D (individuals)	35	3.07
2024		18	3.62
2011	^1D (basal area)	51	2.79
2024		44	3.27
2011	^2D (individuals)	38	0.60
2024		33	0.66
2011	Margalef	33	1.00
2024		8	1.17

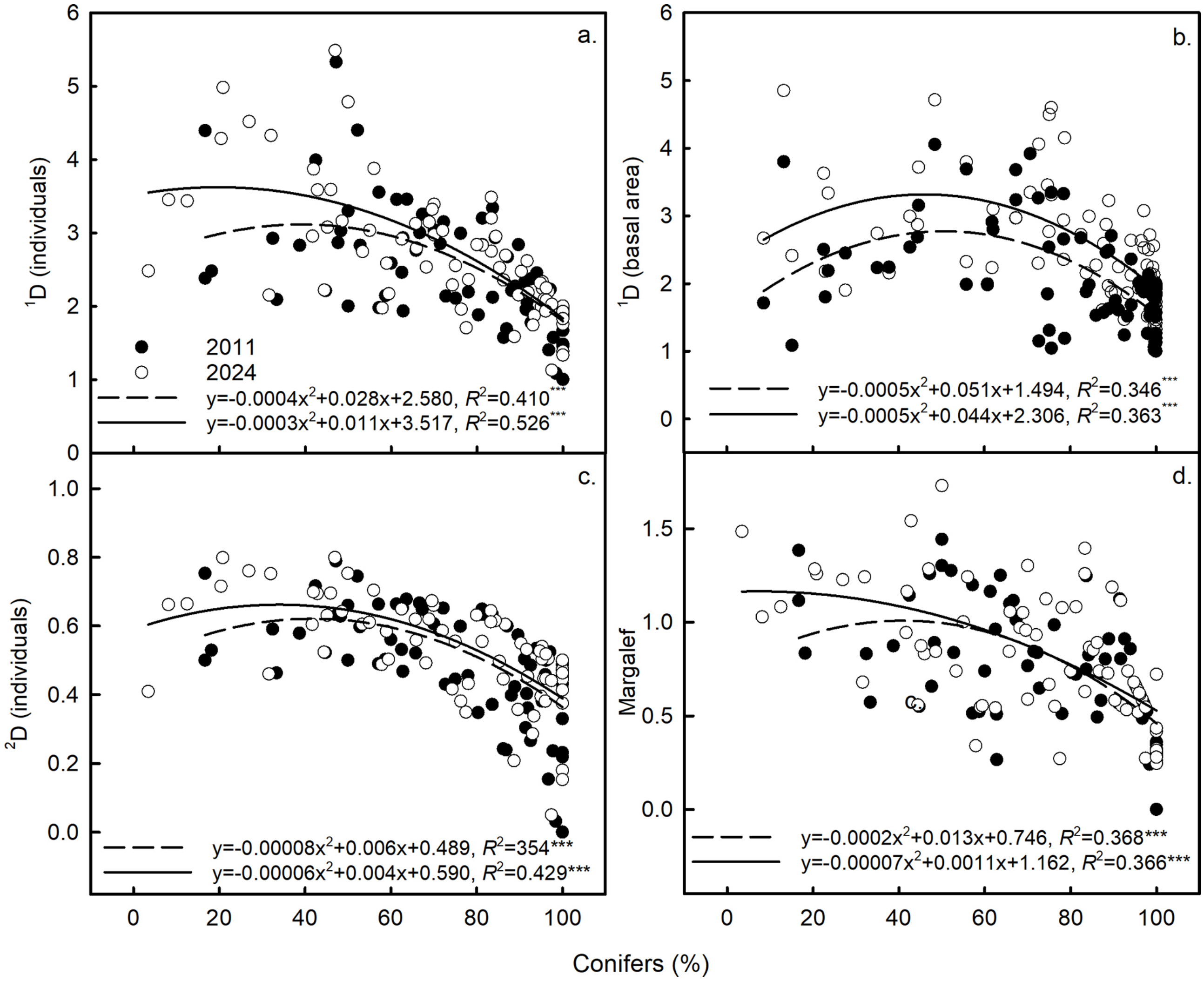

Fig. 7. The relationships between the proportion of evergreen conifers (Picea abies, Pinus sylvestris) and values of Hill numbers (a, b, c) and Margalef (d) index for the observations on the monitoring plots in Wigierski National Park conducted in 2011 and 2024. a. Conifers vs. exponential Shannon index (^1D) calculated with the number of individuals; b. Conifers vs. ^1D calculated with the values of basal area at d.b.h.; c. Conifers vs. inverse Simpson index (^2D); d. Conifers vs. Margalef index. The parabolic equations are fitted. The goodness of fit is assessed with the adjusted coefficient of determination (R^2) with probability (***P < 0.001)

indicate the increased number of common species, i.e. the higher diversity. Notably, the vertex of the ^2D parabola in 2024 corresponded to approximately a 5% reduction in conifer proportion compared to 2011 (Tables 6 and 7, Fig. 7c). The maximum value of the Margalef richness index (*MRI*) increased from 2011 to 2024, reflecting higher species richness relative to total tree abundance (Table 7, Fig. 7d). The vertex of the *MRI* parabola occurred at a noticeably lower proportion of conifers, suggesting that the rise in species richness was primarily due to the greater prevalence of broadleaved species at the expense of evergreen conifers.

Discussion

In Wigry National Park, we have documented a significant increase in dendroflora diversity over a thirteen-year period, from 2011 to 2024. This trend is evidenced by rising values in the exponential Shannon entropy (^1D), inverse Simpson (^2D) and Margalef diversity indices (*MGR*). The increase in tree species diversity reflects significant temporal changes that can be partly attributed to climate change. Our results indicate that natural processes such as self-thinning, progression into higher diameter classes, and tree mortality substantially affect the dynamics of tree species diversity and can interact with broader climate-driven trends.

Additionally, our historical research on the study area, based on the Map of Lake Wigry and Suwałki

Region (1855), Analysis of Wigry National Park's Activities (2023), and Conservation Plan of Wigry National Park (2023), suggests that forest management and active conservation have had only minor effects on tree species diversity within our selected monitoring plots. Nevertheless, the high proportion of old *P. sylvestris* indicates that planting of this species, particularly in the 19th century and between 1914 and 1918, has influenced species composition in WNP (Bogusławski, 2003). In our study, the dominance of conifers is reflected by the high proportion of *P. abies* and *P. sylvestris* in the canopy.

Across selected monitoring plots in WNP, the proportions of cold-tolerant evergreen coniferous species *P. abies* and *P. sylvestris* weighted by the number of individuals or stem density have declined, while warm-tolerant, deciduous broadleaved species have expanded. Additionally, the total number of tree species has grown, including the appearance of the invasive *Q. rubra*.

The relationship between conifer proportion and diversity indices follows a parabolic pattern with diversity increasing to a peak at the vertex of the parabola, after which it declines as conifer dominance rises. This suggests that species richness and evenness are optimal at intermediate levels of conifer presence, with dendroflora diversity in WNP peaking not at the extremes of conifer dominance or absence, but at a balanced midpoint. Specifically, the highest diversity, based on ^1D weighted by the number of individuals, was observed at a conifer composition of approximately 35% in 2011 and 18% in 2024. When ^1D was weighted by basal area, its optimal value increased, while the proportion of conifers decreased from 2011 to 2024, supporting our first hypothesis. In contrast, the proportion of conifers corresponding to the maximum value of the *MRI* dropped sharply in 2024. This suggests that the rise in species richness was driven primarily by an increase in the number of species and decline conifer abundance. When species richness was adjusted for sample size, the optimal conifer proportion associated with the maximum *MRI* value in 2024 was as low as 8%. These results support our first hypothesis.

Our observations suggest that the increased dendroflora diversity has to some extent resulted from the mortality of evergreen conifers, which has opened the forest canopy, allowing more light to reach the forest floor. This has facilitated development of low undergrowth of both shade-tolerant (e.g. *A. platanoides*, *C. betulus* and *T. cordata*) and to lesser extent light-demanding (*P. tremula*) deciduous broadleaved species. Additionally, the microclimatic conditions in canopy gaps formed within the *Tilio cordatae-Carpinetum betuli* forest community supported secondary succession of broadleaved deciduous species and the regeneration of *P. abies*, though not *P. sylvestris*. These gaps generally offer more favourable light, temperature, and moisture conditions for seed germination and seedling establishment than either the shaded canopy interior or fully open areas (Dobrowolska, 2007a; Dobrowolska, 2007b; Dobrowolska & Veblen, 2008). In our study, the *P. sylvestris* natural regeneration was not found. It suggests that highly light demanding seedlings and saplings of this species that typically grow and regenerate in poor soil are outcompeted by other trees and herbaceous fast-growing plants (González-Martínez & Bravo, 2001; Paluch, 2004). Additionally, our observations are concomitant with Sokołowski and Paluch (2004) who stated that in north-eastern Poland, including the WNP, the expansive natural regeneration of *P. abies* did not allow *P. sylvestris* to develop its natural regeneration. *Picea abies* was present at all stages of development, including seedlings, saplings, young trees, mature trees, and old-growth individuals. In contrast, the natural regeneration of other species was less abundant with simpler age structures and fewer individuals in younger developmental stages, unlike the continuous presence of *P. abies* across all stages. Our observation is concomitant with Sokołowski (1980) who stated that a presence of *P. abies* in *Tilio cordatae-Carpinetum betuli* is typical for this community in northeastern Poland. In contrast, *P. sylvestris* is not a typical species for this community (Matuszkiewicz, 2001).

The increased mortality of cold-adapted evergreen conifers is a complex phenomenon, which can be at least partially attributed to their limited adaptation to rising temperatures and more frequent summer droughts. *P. abies*, in particular, is known to be highly sensitive to drought (Treml et al., 2022). Drought is often the primary cause of *P. abies* decline, typically followed by infestations of pathogenic fungi and insects which have been observed in WNP (Łoziński, 2002; Conservation Plan of Wigry National Park, 2023). The decline of conifers, particularly *P. abies*, may be further driven by their high susceptibility to particulate matter (PM) pollution, as shown by Popek et al. (2024), who reported significant PM accumulation and reduced photosynthetic efficiency near the park's boundaries. The source of the mortality of evergreen conifers observed in WNP can be found in their life strategy of retaining multiple cohorts of needles, which proves disadvantageous for survival and growth under a warming climate. However, aging needles are not fully photosynthetically functional (Oluborode et al., 2025). They can be damaged by drought and other stressors. The strategy of deciduous broadleaved species consisting in falling leaves and producing new leaves each year is probably less costly compared to needle long-time retention in evergreen conifers (Song et al., 2022).

Following the recently published study (Dyderski et al., 2025), the tree species which occur in our monitoring plots can be classified into one of three groups: non-threatened (*A. pseudoplatanus, P. avium,* and *C. betulus*), partially threatened (*U. laevis, B. pendula, Q. robur, F. excelsior, T. cordata,* and *A. glutinosa*), and the most threatened (*L. decidua, P. abies,* and *P. sylvestris*). The non-threatened and partially threatened are classified as thermophile species and/or plastic in response to increasing air temperature. For the last group, it has been projected that almost half of the range contraction will occur from 2041 to 2060. However, rapid but modest climate change may create mismatches between the species occurrence in secondary succession and local climate in WNP because of lags in population or species-level adaptation (Robakowski et al., 2012).

The results of this study span a relatively short period of 13 years, which limits our ability to directly correlate ecological indices values and tree measurements with specific climate parameters. Nonetheless, our findings provide evidence that the observed increase in dendroflora diversity marked by a greater proportion of warm-tolerant, deciduous broadleaved species at the expense of evergreen conifers *P. sylvestris* and less *P. abies* has occurred alongside several climate-related changes. These include a roughly two-week extension of the growing season, rising mean annual temperatures, more frequent extreme temperature events, increased drought, and reduced snowfall. These observations suggest that shifts in species composition and population density have been driven at least partly by climatic factors, supporting our second hypothesis. However, significant uncertainty remains, making it difficult to quantify specific risks or impacts, particularly for scattered broadleaved tree species (Hemery et al., 2010). The conservational status of WNP has been crucial for long-term studies on ecological processes allowing to observe an interactive impact of climate change and fluctuations, tree mortality, progression to higher d.b.h. classes and secondary succession of deciduous trees. This would not be possible in intensively managed forests where human activity is an artefact (Fig 1a; Bogusławski, 2003).

Similar to Białowieża National Park, which serves as our benchmark, we observe in WNP the emergence of young generations of broadleaved meso- and eutrophic tree species, accompanied by a simultaneous decline in conifers, namely pine and spruce to a lesser extent. This suggests that the ongoing transformation in tree stand composition in WNP is, to some extent, concurrent with changes observed in the Białowieża Forest (Kowalski, 1994). In old-growth stands of the managed part of the Białowieża Forest between 1949 and 2006, *C. betulus* and *T. cordata* were even regarded as expansive species, *P. abies* was considered stable, and *P. sylvestris* was classified as declining (Drozdowski et al., 2020). Our findings are consistent with long-term monitoring results from the Białowieża Forest, indicating that in WNP, *C. betulus* and *T. cordata* have high growth potential, while *P. sylvestris* is in decline.

Our study offers valuable insights into the predicted changes in dendroflora diversity in WNP in response to local climate fluctuations. The findings provide evidence to support the biodiversity conservation and the ecological processes driving the secondary succession of deciduous broadleaved trees in the park. The established network of monitoring plots in WNP, a biodiversity hotspot in north-eastern Poland, creates a unique opportunity for long-term observation of shifts in the dendroflora composition and other forest-dwelling organisms (Behnke-Borowczyk et al., 2023). In the long term, we recommend the continued monitoring of dendroflora diversity and growth in WNP to improve the modelling of forest tree responses to global climate change.

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Contribution

Conceptualization: PR, WK; Methodology: RJ, PR; Formal analysis: PR, RJ; Investigation: RJ, MB, BB, MD, MH-K, RK, AŁ, JSz, MZ, AW, RP, AP, WK; Writing – original draft preparation: PR; Writing – review and editing: RJ; MB, BB, MD, MH-K, RK, AŁ, JSz, MZ, AW, RP, AP, WK; Funding acquisition: WK; Supervision: WK

References

Analysis of Wigry National Park's Activities (2021) Wigry National Park, Krzywe. https://wigpn.gov.pl/pliki-do-pobrania/otworz/ea654cbd-95f3-454e-93fa-a3b5d6b61d1a.pdf.

Analysis of Wigry National Park's Activities (2023). Wigry National Park, Krzywe. https://wigpn.gov.pl/pliki-do-pobrania/otworz/e25d4d55-d7bc-4ca8-87ab-b3fc062777dc.pdf.

Bader MKF, Leuzinger S, Keel SG, Siegwolf RTW, Hagedorn F, Schleppi P & Körner Ch (2013) Central European hardwood trees in a high-CO_2 future: synthesis of an 8-year forest canopy CO_2 enrichment project. Journal of Ecology 101: 1509–1519. doi:10.1111/1365-2745.12149.

Bates D, Mächler M, Bolker B & Walker S (2015) Fitting linear mixed-effects models using Ime4. Journal of Statistical Software 67: 1–48. doi:10.18637/jss.v067.i01.

Behnke-Borowczyk J, Korzeniewicz R, Łukowski A, Baranowska M, Jagiełło R, Bułaj B, Hauke-Kowalska M, Szmyt J, Behnke JM, Robakowski P & Kowalkowski W (2023) Variability of functional groups of rhizosphere fungi of Norway spruce (*Picea abies* (L.) H.Karst.) in the boreal range: The Wigry National Park, Poland. International Journal of Molecular Sciences 24: 12628. doi:10.3390/IJMS241612628.

Bernadzki E, Bolibok L, Brzeziecki B, Zajączkowski J & Żybura H (1998) Compositional dynamics of natural forests in the Bialowieza National Park, northeastern Poland. Journal of Vegetation Science 9: 229–238. doi:10.2307/3237122.

Bogusławski Z (2003) Natural forests – history and current state. Przyroda i Krajobraz 3. https://www.wigry.org.pl/kwartalnik/nr11_lasy.htm.

Brzeziecki B (2017) Long-term dynamics of trees and stands in the Strict Reserve of Białowieża National Park: Forests of the Strict Reserve of Białowieża National Park (ed. by A Keczyński) Białowieski Park Narodowy, Białowieża, pp. 94–125.

Brzeziecki B & Kienast F (1994) Classifying the life-history strategies of trees on the basis of the Grimian model. Forest Ecology and Management 69: 167–187. doi:10.1016/0378-1127(94)90227-5.

Chao A, Gotelli N, Hsieh TC, Sander EL & Ma KH (2014) Rarefaction and extrapolation with Hill numbers: a framework for sampling and estimation in species diversity studies. Ecological Monographs 84: 45–67. doi:10.1890/13-0133.1.

Conservation Plan of Wigry National Park (2016) https://www.wigry.org.pl/inf_i_rozw/plany/materialy.htm.

Conservation Plan of Wigry National Park (2023) Project of the Conservation Plan of Wigry National Park. https://wigpn.gov.pl/plan-ochrony.

Danielewicz W & Pawlaczyk P (2004) Guidelines for the protection of habitats and species of Natura 2000 – methodological manual: Forests and woodlands (ed. by J Herbich) Warszawa, Ministerstwo Środowiska.

Dobrowolska D (2007a) Dynamika luk w lasach a odnowienie naturalne drzew. Leśne Prace Badawcze 1: 97–111.

Dobrowolska D (2007b) Role of gaps in the regeneration of mixed stands in the Jata reserve. Sylwan 151: 14–25.

Dobrowolska D & Veblen TT (2008) Treefall-gap structure and regeneration in mixed *Abies alba* stands in central Poland. Forest Ecology and Management 255: 3469–3476. doi:10.1016/j.foreco.2008.02.025.

Drozdowski S, Brzeziecki B, Żybura H, Żybura B, Gawron L, Buraczyk W, Zajączkowski J, Bolibok L, Szeligowski H, Bielak K & Widawska Z (2020) Long-term dynamics of old-growth stands in the managed part of the Białowieża Forest: expansive and declining species*: Two Centuries of the Białowieża Forest in Sylwan Journal (ed. by A Grzywacz) Commissioned by the Directorate-General of the State Forests, Warszawa, pp. 387–397.

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

Dyderski MK, Paź-Dyderska S, Jgodziński A & Puchałka R (2025) Shifts in native tree species distributions in Europe under climate change. Journal of Environmental Management 373: 123504. doi:10.1016/J.JENVMAN.2024.123504.

Gazda A, Kościelniak P, Hardy M, Muter E, Kędra K, Bodziarczyk J, Frączek M, Chwistek K, Różański W & Szwagrzyk J (2019) Upward expansion of distribution ranges of tree species: Contrasting results from two national parks in Western Carpathians. Science of the Total Environment 653: 920–929. doi:10.1016/j.scitotenv.2018.10.360.

González-Martínez SC & Bravo F (2001) Density and population structure of the natural regeneration of Scots pine (*Pinus sylvestris* L.) in the High Ebro Basin (Northern Spain). Annals of Forest Sciences 58: 277–288. doi:10.1051/forest:2001126.

Gougherty AV, Keller SR & Fitzpatrick MC (2021) Maladaptation, migration and extirpation fuel climate change risk in a forest tree species. Nature Climate Change 11: 166–171. doi:10.1038/s41558-020-00968-6.

Górniak A (2021) Klimat województwa podlaskiego w czasie globalnego ocieplenia. Wydawnictwo Uniwersytetu w Białymstoku, Białystok.

Grime JP (1977) Evidence for the existence of three primary strategies in plants and its relevance to ecological and evolutionary theory. The American Naturalist 111: 1167–1194.

Hawkins E & Sutton R (2012) Time of emergence of climate signals. Geophysical Research Letters 39: 1–6. doi:10.1029/2011GL050087.

Hemery GE, Clark JR, Aldinger E, Claessens H, Malvolti ME, O'connor E, Raftoyannis Y, Savill PS & Brus R (2010) Growing scattered broadleaved tree species in Europe in a changing climate: a review of risks and opportunities. Forestry 83: 65–81. doi:10.1093/forestry/cpp034.

Heuertz M, Carvalho SB, Galindo J, Rinkevich B, Robakowski P, Aavik T, Altinok I, Barth JMI, Cotrim H, Goessen R, González-Martínez SC, Grebenc T, Hoban S, Kopatz A, McMahon BJ, Porth I, Raeymaekers JAM, Träger S, Valdecantos A, Vella A, Vernesi C & Garnier-Géré P (2023) The application gap: genomics for ecosystem service management. Biological Conservation 278: 109883. doi:10.1016/j.biocon.2022.109883.

Hill MO (1973) Diversity and evenness: A unifying notation and its consequences. Ecology 54: 427–432. doi:10.2307/1934352.

IPCC (2023) Summary for policymakers: Climate Change 2023: Synthesis Report. Contribution of Working Groups I, II and III to the Sixth Assessment Report of the Intergovernmental Panel on Climate Change (ed. by H Lee & J Romero) IPCC, Geneva, Switzerland, pp. 1–34. doi:10.59327/IPCC/AR6-9789291691647.001.

Jost L (2006) Entropy and diversity. Oikos 113: 363–375. doi:10.1111/j.2006.0030-1299.14714.x.

Kejna M & Rudzki M (2021) Spatial diversity of air temperature changes in Poland in 1961–2018. Theoretical and Applied Climatology 143: 1361–1379. doi:10.1007/s00704-020-03487-8.

Kowalski M (1994) Zmiany składu gatunkowego lasów na tle zmian klimatu w ostatnich dwóch stuleciach. Sylwan 138: 33–44.

Kumar P, Dobriyal M, Kale A, Pandey AK, Tomar RS & Thounaojam E (2022) Calculating forest species diversity with information-theory based indices using sentinel-2A sensor's of Mahavir Swami Wildlife Sanctuary. PloS ONE 17: e0268018. doi:10.1371/journal.pone.0268018.

Kumarathunge DP, Medlyn BE, Drake JE, Tjoelker MG, Aspinwall MJ, Battaglia M, Cano FJ, Carter KJ, Cavaleri MA, Cernusak LA, Chambers JQ, Crous KY, De Kauwe MG, Dillaway DN, Dreyer E, Ellsworth DS, Ghannoum O, Han Q, Hikosaka K, Jensen AM, Kelly JWG, Kruger EL, Mercado LM, Onoda Y, Reich PB, Rogers A, Slot M, Smith NG, Tarvainen L, Tissue DT, Togashi HF, Tribuzy ES, Uddling J, Vårhammar A, Wallin G, Warren JM & Way DA (2019) Acclimation and adaptation components of the temperature dependence of plant photosynthesis at the global scale. New Phytologist 222: 768–784. doi:10.1111/nph.15668.

Lindner M, Maroschek M, Netherer S, Kremer A, Barbati A, Garcia-Gonzalo J, Seidl R, Delzon S, Corona P, Kolströma M, Lexer MJ & Marchetti M (2010) Climate change impacts, adaptive capacity, and vulnerability of European forest ecosystems. Forest Ecology and Management 259: 698–709. doi:10.1016/j.foreco.2009.09.023.

Lüdecke D, Shachar B, Patil I, Waggoner P & Makowski D (2021) performance: An R package for assessment, comparison and testing of statistical models. Journal of Open Source Software 6: 3139. doi:10.21105/joss.03139.

Łoziński J (2002) Changes of the Norway spruce strictly protected forests in the Wigry National Park. Prace Instytutu Badawczego Leśnictwa A926/930: 53–74.

Map of Lake Wigry and the Suwałki Region (1855) Lithuanian State Historical Archives, Vilnius. f. 1604, ap. 1, b. 3169.

Margalef R (1958) Information theory in ecology. General Systems 3: 36–71.

Matuszkiewicz JM (2001) Forest communities of Poland. PWN, Warszawa.

Matuszkiewicz JM & Wolski J (2023) Potential natural vegetation of Poland (vector version). IGiPZ PAN, Warszawa.

Migaszewski ZM, Gałuszka A & Pasławski P (2004) Baseline element concentrations in soils and plant bioindicators of selected national parks of Poland. Geological Quarterly 48: 383–394.

Milesi P, Berlin M, Chen J, Orsucci M, Jansson G, Karlsson B & Lascoux M (2018) Assessing the potential for assisted gene flow using past introduction of Norway spruce in Southern Sweden: Local adaptation and genetic basis of quantitative traits in trees. Evolutinary Applications 2: 1946–1959. doi:10.1111/eva.12855.

Myers N, Mittermeier RA, Mittermeier CG, da Fonseca GAB & Kent J (2000) Biodiversity hotspots for conservation priorities. Nature 403: 853–858. doi:10.1038/35002501.

Oddou-Muratorio S, Davi H & Lefèvre F (2020) Integrating evolutionary, demographic and ecophysiological processes to predict the adaptive dynamics of forest tree populations under global change. Tree Genetics & Genomes 16: 67. doi:10.1007/s11295-020-01451-1.

Oksanen J, Simpson G, Blanchet F, Kindt R, Legendre P, Minchin P, O'Hara R, Solymos P, Stevens M, Szoecs E, Wagner H, Barbour M, Bedward M, Bolker B, Borcard D, Carvalho G, Chirico M, De Caceres M, Durand S, Evangelista H, FitzJohn R, Friendly M, Furneaux B, Hannigan G, Hill M, Lahti L, McGlinn D, Ouellette M, Ribeiro Cunha E, Smith T, Stier A, Ter Braak C, Weedon J & Borman T (2025) Vegan. Community Ecology Package. https://CRAN.R-project.org/package=vegan.

Oluborode J, Chadżinikolau T, Formela-Luboińska M, Ye Zi-Piao & Robakowski P (2025) Adaptive significance of age- and light-related variation in needle structure, photochemistry, and pigments in evergreen coniferous trees. Photosynthesis Research 163: 3. doi:10.1007/S11120-024-01125-2.

Paluch R (2004) Stan, warunki i problemy odnowienia naturalnego sosny w Puszczy Białowieskiej*. Sylwan 11: 9–21.

Popek R, Przybysz A, Łukowski A, Baranowska M, Bułaj B, Hauke–Kowalska M, Jagiełło R, Korzenieiwcz R, Moniuszko H, Robakowski P, Zadworny M & Kowalkowski W (2024) Shields against pollution: phytoremediation and impact of particulate matter on trees at Wigry National Park, Poland. International Journal of Phytoremediation 27: 448–461. doi:10.1080/15226514.2024.2426771.

R Core Team (2025) R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. https://www.R-project.org/.

Reich PB, Sendall KM, Rice K, Rich RL, Stefanski A, Hobbie SE & Montgomery RA (2015) Geographic range predicts photosynthetic and growth response to warming in co-occurring tree species. Nature Climate Change 5: 148–152. doi:10.1038/nclimate2497.

Reich PB, Sendall KM, Stefanski A, Wei X, Rich RL & Montgomery RA (2016) Boreal and temperate trees show strong acclimation of respiration to warming. Nature 531: 633–636. doi:10.1038/nature17142.

Reich PB & Oleksyn J (2008) Climate warming will reduce growth and survival of Scots pine except in the far north. Ecology Letters 11: 588–597. doi:10.1111/j.1461-0248.2008.01172.x.

Robakowski P, Li Y & Reich PB (2012) Local ecotypic and species range-related adaptation influence photosynthetic temperature optima in deciduous broadleaved trees. Plant Ecology 213: 113–125. doi:10.1007/s11258-011-0011-3.

Sendall KM, Reich PB, Zhao Ch, Jihua H, Wei X, Stefanski A, Rice K, Rich RL & Montgomery RA (2015) Acclimation of photosynthetic temperature optima of temperate and boreal tree species in response to experimental forest warming. Global Change Biology 21: 1342–1357. doi:10.1111/gcb.12781.

Sokołowski AW (1980) Zbiorowiska leśne północno-wschodniej Polski. Monographiae Botanicae 60: 5–85.

Sokolowski AW (1988) Flora roślin naczyniowych Wigierskiego Parku Narodowego. Parki Narodowe i Rezerwaty Przyrody 9: 5–84.

Sokołowski WA & Paluch R (2004) Wpływ sztucznego odnawiania drzewostanów w borze mieszanym na skład zbiorowisk leśnych w Wigierskim Parku Narodowym. Sylwan 12: 48–57.

Song Y, Sterck F, Zhou X, Liu Q, Kruijt B & Poorter L (2022) Drought resilience of conifer species is driven by leaf lifespan but not by hydraulic traits. New Phytologist 235: 978–992. doi:10.1111/NPH.18177.

Svenning J & Skov F (2005) The relative roles of environment and history as controls of tree species composition and richness in Europe. Journal of Biogeography 32: 1019–1033. doi:10.1111/j.1365-2699.2005.01219.x.

Thuiller W, Lavorel1 S, Sykes MT & Araújo MB (2006) Using niche-based modelling to assess the impact of climate change on tree functional diversity in Europe. Diversity and Distributions 12: 49–60. doi:10.1111/j.1366-9516.2006.00216.x.

Treml V, Mašek J, Tumajer J, Rydval M, Čada V, Ledvinka O & Svoboda M (2022) Trends in climatically driven extreme growth reductions of *Picea abies* and *Pinus sylvestris* in Central Europe. Global Change Biology 28: 557–570. doi:10.1111/gcb.15922.

Turcotte MM & Levine JM (2016) Phenotypic Plasticity and Species Coexistence. Trends in Ecology & Evolution 31: 803–813. doi:10.1016/j.tree.2016.07.013.

Zarzycki K, Trzcińska-Tacik H, Różański W, Szeląg Z, Wołek J & Korzeniak U (2002) Ecological indicator values of vascular plants of Poland. Instytut Botaniki im. W. Szafera PAN, Kraków.