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High tree host diversity buffers the effect of *Fraxinus excelsior* dieback on epiphytic bryophytes composition in the Białowieża Primeval Forest

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Abstract: Invasions are one of main drivers transforming the functions of forest ecosystems. The invasion of alien fungus *Hymenoscyphus fraxineus* is still reducing the abundance of *Fraxinus excelsior* throughout temperate Europe. *F. excelsior* is a tree species belonging to the group of foundation species for numerous epiphytic species. We studied the effects of *F. excelsior* decline on epiphytic bryophytes in the Białowieża Primeval Forest. In this forest human interference is limited, allowing us to register the natural dynamics of ash-dependent bryophyte communities. *F. excelsior* decline was discovered in the Białowieża Primeval Forest in 1998, and in 2016 we resurveyed a historical survey of epiphytic bryophytes, i.e. shortly before the dieback process started. Using ordination methods and mixed-effect models we assessed shifts in epiphyte bryophytes composition over time and amongst the plots with (i) historical and recent presence of *F. excelsior*, (ii) with recent extinction of *F. excelsior*, and (iii) absence of *F. excelsior* both historically and recently, as well as at the level of alternative tree hosts employing the paired Mann-Whitney and *t*-tests. *F. excelsior* dieback did not influence the species composition of bryophytes associated with this tree host. Despite the drastic reduction in living *F. excelsior* trees (85%), overall the species composition, species richness and Shannon index of *F. excelsior*-dwelling bryophytes did not shift significantly between two sampling periods. Similarly weak changes over time we reported for the bryophytes' community weighted means of ecological indicator values. Equally subtle temporal shifts in epiphytes' biodiversity were observed amongst the plots with the presence, absence, and extinction of ash, likely due to the relatively high diversity of available alternative hosts. *F. excelsior*-associated epiphytic bryophytes were able to exploit other niches in the microhabitat-heterogeneous Białowieża Forest ecosystem, and thus far have not suffered a reduction in biodiversity parameters at the scale of our survey. High diversity of alternative host tree species, with particular emphasis on the occurrence of pioneer trees (i.e. *B. pendula* and *P. tremula*), may maintain the epiphytic bryophyte communities, which themselves may be able to act as a source for the recovery of *F. excelsior*-affiliated epiphyte populations.

Keywords: ancient woodland, epiphytes, host trees, *Hymenoscyphus fraxineus*, resampling

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Introduction

Over the past seven decades, climate warming, land-use change, urbanization, eutrophication, and biological invasions have been pointed out as the main anthropogenic drivers of compositional shifts in plant communities (Vitousek et al., 1997; Chapin III et al., 2000; Steffen et al., 2015; Steinbauer et al., 2018). For tree species, invasions by alien pathogen species are considered one of the main drivers of extinctions and losses of diversity worldwide (Najberek et al., 2022). Numerous tree species are of particular importance to ecosystem functions and services, due to their role in shaping other species' life cycles and creation of suitable habitats for various taxonomical groups of organisms (Ellison et al., 2005).

One of the trees belonging to the group of foundation species is European ash (*Fraxinus excelsior* L.), in Central Europe typically occurring in riparian and alder carr forests. Due to their high abundance, *F. excelsior* trees shape the functions and dynamics of these forest communities (Hunter et al., 2017), one of the most important hotspots of biodiversity in the temperate zone of climate (Richardson et al., 2007). *F. excelsior* constitutes source habitat for a large diversity of birds (Wesołowski et al., 2015), invertebrates (Kennedy & Southwood, 1984), fungi, and lichens (Pentecost, 2014; Preikša et al., 2016). *F. excelsior* trees are also important hosts for epiphytic bryophytes (Lõhmus & Runnel, 2014; Pentecost, 2014; Wierzcholska et al., 2018), owing to their long lifespan, large size (Faliński, 1977), close-to-neutral bark pH, and high water capacity (Barkman, 1958). Therefore, threats to *F. excelsior* are threats to its dependent species, potentially causing a cascade of negative effects on biodiversity.

Currently, the most important threat to *F. excelsior* is invasion of a nonnative fungus *Hymenoscyphus fraxineus*, with a natural geographical range covering eastern Japan, Korea, and northeast China (Baral & Bemmann, 2014). Infection by *H. fraxineus* causes wilting and loss of leaves, darkening of wood, necrosis of stems and entire branches, and finally leads to death of *F. excelsior* trees (Baral et al., 2014; Gross et al., 2014). The first record of this pathogenic fungus in Europe was made in Poland in 1992 (Kowalski, 2006), and it has since then expanded to other areas in Europe, including Central and Eastern Europe, the British Isles, and Scandinavia (e.g. Schumacher et al., 2007; Talgø et al., 2009; Timmermann et al., 2011; Mitchell et al., 2014). Its expansion is the main reason for the substantial decline in *F. excelsior* abundance throughout Europe with losses of this tree often exceeding 90% (Cholewińska et al., 2018).

The dieback of *F. excelsior* may cause a serious loss of biodiversity associated with this tree, especially including the species for which *F. excelsior* is the obligatory or facultative host (Mitchell et al., 2016). Such negative trends have been demonstrated in managed forests and monocultures by Lõhmus and Runnel (2014). In these tree stands, expansion of *H. fraxineus* on ash resulted in the creation of large meadow-like openings (Heilmann-Clausen et al., 2013), which in turn led to the drastic changes in habitat conditions, e.g. higher light availability and evaporation (Mitchell et al., 2016). Some of the *F. excelsior*-dwelling species may adapt to newly established habitat conditions, colonizing alternative host trees in the neighborhood, but some taxa may not find suitable alternative hosts, nor follow the rapid shifts in environmental conditions, and thus become locally extinct (Mitchell et al., 2014; Mitchell et al., 2016).

Epiphytic bryophytes are one of the most threatened groups of cryptogams (Wierzcholska et al., 2020). Due to their specific physiological and biological traits (narrow ecological requirements), epiphytic bryophytes serve as indicators of forest continuity, as well as indicators of changes in the environment (e.g. Proctor, 2011; Slack, 2011; Wierzcholska et al., 2018). The life-span of their tree hosts is the crucial factor determining the occurrence patterns of this functional group of organisms (Snäll et al., 2005).

Primeval forest ecosystems with a wide spectrum of specific microclimates, and a high number of habitats shaped by a high diversity of forest vegetation and tree hosts therefore offer the best opportunity to understand the fundamental dynamics of the epiphytic communities, as such ecosystems offer the necessary complexity of available niches for specialists. In particular, we propose that primeval forests with high complexity of tree stands provide the opportunity for novel perspectives on compositional dynamics of epiphytic bryophytes under the impact of losses of foundation tree species. One example of such forest ecosystems is the Białowieża Primeval Forest, considered the most close-to-natural forest in the temperate climate zone of Europe (Faliński, 1986; Jaroszewicz et al., 2019). As such, the diversity of trees occurring there in numerous combinations and ages is higher than in managed forests (Bobiec et al., 2000). The *F. excelsior* population of the Białowieża Forest has decreased by two-thirds over the past two decades, with even greater reductions in typical hydrogenic communities (Keczyński, 2005; Cholewińska et al., 2018), placing *F. excelsior*-dwelling species in a precarious situation. However, the knowledge of the consequences of *F. excelsior* dieback for epiphyte diversity in protected forest areas is still limited (Łubek et al., 2020). Our study may address two of the recent '20 priority research questions' in ecology (Musche et al., 2019): 'How do changes in species diversity, functional diversity, and community composition affect ecosystem functioning?' and 'What are the major impacts of invasion by alien species on ecosystems and on society, and what is their magnitude compared to other drivers of global change?'.

We studied the effects of *F. excelsior* decline in a close-to-natural forest ecosystem, in which human interference is strictly limited. Owing to a historical survey, which took place in 1992 shortly before the dieback process started, and the lack of modification of forest communities by forest management activities, we registered the response of *F. excelsior*-inhabiting bryophytes. We aimed to answer the following questions: a) How *F. excelsior* dieback would influence the species composition of bryophytes over time? b) what is the role of other tree hosts in the long-term persistence of *F. excelsior*-affiliated epiphytic bryophytes, and c) does the *F. excelsior* dieback pose a threat to the biodiversity of bryophytes in the close-to-natural forest?

Materials and methods

Study area and study design

Our study was carried out in the strictly protected part of the Białowieża National Park (NE Poland; Fig. 1). The strictly protected area of the national park is the best-preserved area of mixed deciduous forests in the European lowlands (Peterken, 1996), comprising 47 km^2 of the 6,700 km^2 national park. The forest is a flagship site for forest conservation in Europe, and the UNESCO world heritage site since 1979. It was never commercially logged, and the area has been covered by forest ecosystems for the last several thousand years (Faliński, 1986; Latałowa et al., 2016). The survey was conducted in the mosaic of six forest communities representing mixed-deciduous forests of the temperate climate (*Carici elongatae-Alnetum, Circeao-Alnetum, Peucedano-Pinetum, Pino-Quercetum, Querco-Piceetum*, and *Tilio-Carpinetum*).

We resurveyed epiphytic bryophytes on the 144 permanent plots established in the "CRYPTO" project, each 100 m × 100 m (1 ha each) with permanently marked corners, which allowed us the conductance of highly precise resurvey. Previous sampling on the same plots took place during the CRYPTO project, about 25 years ago (Faliński & Mułenko, 1997), i.e. over the years 1989–1992 (hereafter referred to as the "1992 survey") by Klama (1995) and Żarnowiec (1995). During the vegetation seasons of 2014, 2015, and 2016 (hereafter referred to as the "2016 survey") we resampled bryophytes on the same area, and used the same methods as was used in the previous survey. We excluded from initial dataset (n=288 plots) a total of 96 plots: (i) representing coniferous forest communities (n=80 plots; i.e. *Peucedano-Pinetum, Pino-Quercetum,* and *Querco-Piceetum*) with low chance for the occurrence of *F. excelsior* there due to unsuitable habitat conditions, as well as 16 plots with recent colonization of ash (*F. excelsior* recorded in 2016, but not occurring in 1992) due to low sample size. We divided plots into three categories (total n for both sampling periods = 192 plots): (i) with a presence of *F. excelsior* (both in 1992 and 2016; n = 86 plots), (ii) with recent extinction of *F. excelsior* (recorded as dead trees in 2016; n = 42 plots), and (iii) absence of *F. excelsior* (both in 1992 and 2016; n = 64 plots). Each study plot was carefully searched for bryophytes (one plot – one day). Once a plot had been completed, the abundance for each bryophyte species was assigned on a three-degree scale: 1 – rare (<5 records/plot), 2 – frequent (6–10 records/plot), 3 – common (>10 records/plot). Epiphytes were recorded on tree trunks from the base of the tree to 2 m above the ground. For each bryophyte species, the tree host species was noted. The following tree hosts were distinguished: *Acer platanoides, Alnus glutinosa, Betula pendula, Carpinus betulus, Corylus avellana, F. excelsior, Picea abies, Pinus sylvestris, Populus tremula, Quercus robur, Tilia cordata,* and *Ulmus glabra*.

We characterized the ecological requirements of epiphytic bryophyte species for light, temperature, moisture, and reaction (pH; corresponding to substrate fertility), using the ecological indicator values (EIVs) provided by Ellenberg et al. (1992). These

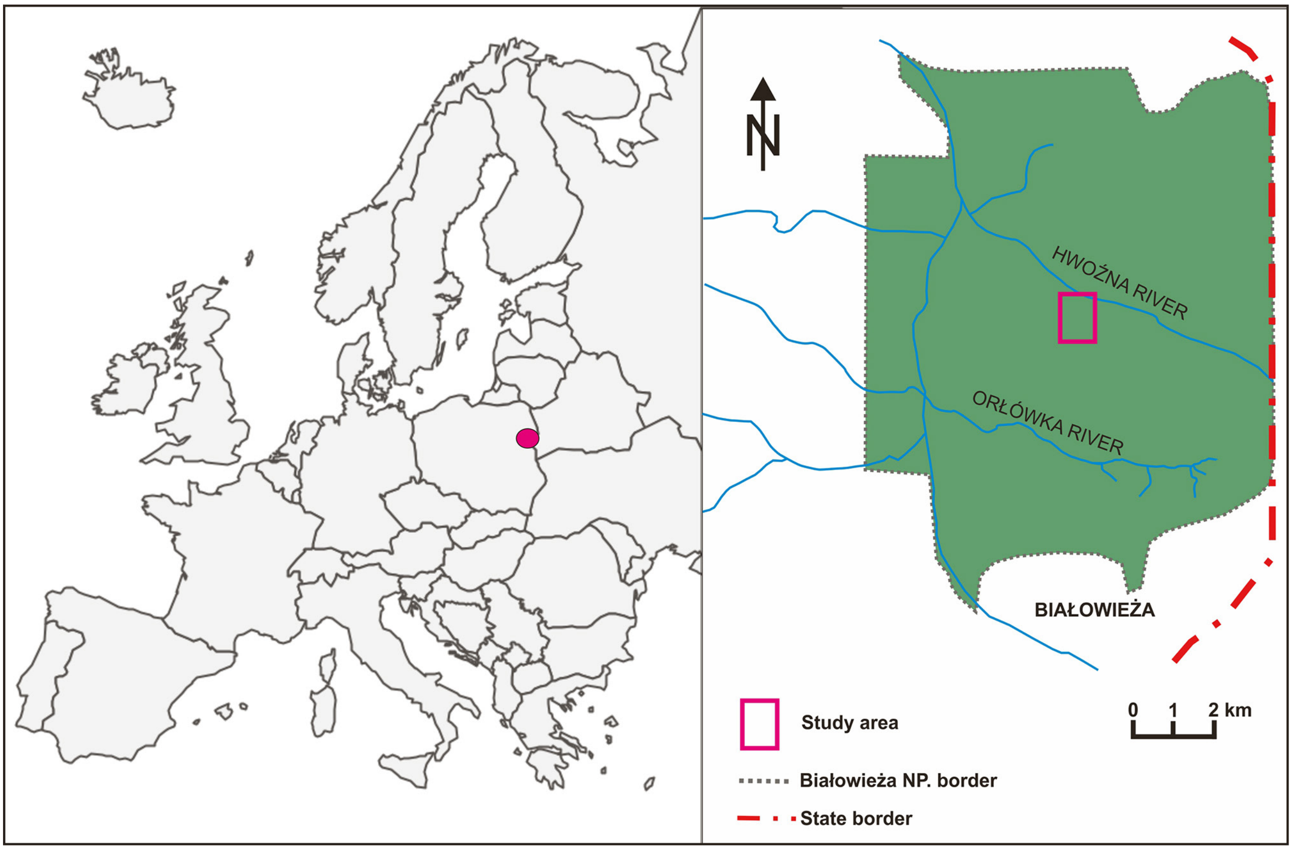

Fig. 1. The study area (the central point coordinates N52.7677, E23.8666) in the Białowieża National Park, NE Poland

indicators illustrate the species' realized niche forming as the outcome of joint impacts of environmental gradients acting over time (Chytrý et al., 2009; Smart & Scott, 2009). For each historical and resampled plot representing each of three categories of *F. excelsior* occurrence status, as well as for each tree host surveyed in 1992 and resurveyed in 2016, we calculated the community weighted mean values (CWMs: mean values weighted by the abundance score of the individual species in the community) of the bryophyte species' EIVs (light, temperature, moisture and substrate reaction), and two metrics of taxonomic diversity (species richness and Shannon index).

Data analyses

We performed all statistical analyses using R (version: 4.3.0; R Core Team, 2023). To determine the main patterns of changes in species composition of epiphytic bryophytes at a plot level between two sampling periods (1992 vs 2016), and amongst (i) plots with extinction of *F. excelsior*, (ii) plots that never contained *F. excelsior* and (ii) plots still containing *F. excelsior* after 23 years from first sampling period we used the Principal Components Analysis (PCA; gradient length = 1.60), implemented in the *vegan::rda()* function (Oksanen et al., 2022). To avoid overlooking possibly important and biologically interpretable results we did not include the downweighting of rare species occurring in low abundances (>5%). Using the *vegan::envfit()* function (Oksanen et al., 2022), we fitted parameters of bryophyte species diversity (i.e. species richness and Shannon index) and CWMs of bryophytes' EIVs (i.e. light, temperature, moisture, and reaction) as passive vectors to the ordination results. To check the importance of each vector in describing the species composition of plots, for each vegetation parameter we calculated the determination coefficient R^2 and P-value using a permutation test with 999 iterations (*vegan::envfit()* function; Oksanen et al., 2022).

To examine shifts in characteristics of epiphytes vegetation (i.e. species richness, Shannon index, and CWMs of EIVs) between two sampling periods, as well as amongst the plots with extinction, presence, and absence of *F. excelsior*, we used mixed effect models. To account for the influence of plot-specific factors (e.g. linked with differences in availability of substrates and tree hosts, microclimate, and microhabitat heterogeneity) on the obtained results, we adopted the plot identity as a random factor. We utilized the *MuMIn::r.squaredGLMM()* function (Bartoń, 2024) to compute the marginal (R^2_m) and conditional coefficient (R^2_c) of determination for all the models performed. R^2_m quantifies the amount of variance explained exclusively by fixed effects, whereas R^2_c

quatifies the amount of variance explained by both random and fixed effects. The disparity between R_c^2 and R_m^2 represents the amount of variance explained solely by the random factor. To examine whether changes in bryophyte vegetation parameters over time were influenced by *F. excelsior* dieback, we added an interaction between the time of sampling and the presence of *F. excelsior* in plots as another predictor in models. To assess differences in species richness (discrete variable) we employed the generalized linear mixed effect model with Conway-Maxwell-Poisson distribution of response variable (*glmmTMB::glmmTMB()* function; Brooks et al., 2024), as regarding to nonparametric dispersion test (dispersion value = 0.74; $P = 0.008$), implemented in the *DHARMa::simulateResiduals()* and *DHARMa::testDispersion()* functions (Hartig, 2022). For the remaining characteristics of bryophyte vegetation (continuous variables), we employed mixed effect linear models (*glmmTMB::glmmTMB()* function; Brooks et al., 2024), assuming the close-to-normal distribution of response variables. We evaluated the results of mixed effect models using the *car::Anova()* function (Fox et al., 2024) and the Tukey posteriori test implemented in the *multcomp::cld()* function (Horthorn et al., 2024).

To explore general changes in species richness of bryophytes over time at the tree host level, we employed the paired Mann-Whitney test, assuming the non-normal distribution of the response variable. To assess temporal shifts in the Shannon index and CWMs of EIVs at the level of tree hosts, we used a paired *t*-test, assuming the close-to-normal distribution of response variables. To assess the main patterns of shifts in species composition of epiphytes among tree hosts over time, we employed PCA ordination (gradient length = 2.38) with the same (as regarded to the plot level) passive projection of bryophyte vegetation characteristics evaluated by R^2 coefficients and *P*-values, calculated using a permutation test with 999 iterations (*vegan::envfit()* function; Oksanen et al., 2022).

Results

According to the results of PCA ordination, we observed relatively weak and plot-specific changes in species composition of bryophytes over time, with *F. excelsior* occurrence status identified as more important factor shaping the structure of the epiphytes' assemblages (Fig. 2). The gradient along PCA axis 1 ordered plots along species' moisture requirements (CWM of moisture EIV), as well as species richness and Shannon index, explaining about 19% of variability in species composition. The gradient along PCA2 axis ordered plots depending on the occurrence of *F. excelsior* and species' temperature demands (CWM of temperature EIV), explaining about 15% of variance variability, and revealing partial compositional continuum among plots with the extinction of *F. excelsior*, and those that never contained or still contain *F. excelsior* after 23 years from first sampling period. The species composition of most of the plots containing *F. excelsior* was shaped mostly by high values of CWM of temperature EIV, while plots with extinction and absence of *F. excelsior* were characterized by lower values of this parameter (Supplementary Table 1).

Considering the results of almost all mixed effect models (apart from species richness), the amount of variability explained by random factors linked with plot identity was higher (ranging from 54% for the Shannon index and CWM of light EIV to 88% in the case of CWM of reaction EIV) than explained by fixed effects (ranging from 3% for CWM of reaction EIV to 16% in case of Shannon diversity index). From all vegetation characteristics analyzed, only CWM of temperature EIV was statistically significantly influenced by the interaction between the time of sampling and the presence of *F. excelsior* in plots. The differences in the remaining parameters of epiphyte vegetation were explained by the single or additive effects of both predictors mentioned above (Table 1).

Independently from the year of sampling, mean values of species richness and Shannon index were statistically significantly higher in plots with the presence (of about 5.60 and 0.16 on average, respectively) and extinction of *F. excelsior* (of about 4.30 and 0.12 on average, respectively) compared to plots with an absence of this tree host. Mean values of CWM of moisture EIV were statistically significantly higher in plots with *F. excelsior* presence, compared to plots with the absence of this tree host (of about 0.13 on average), and did not differ statistically significantly when compared to plots with *F. excelsior* extinction (independently from the year of sampling). Although statistical significance, the differences in mean values of CWM of temperature EIV amongst the plots with different statuses of *F. excelsior* occurrence were weak (independently from the year of sampling). Mean values of CWM of temperature EIV were statistically significantly higher in historical than resampled plots with an absence of *F. excelsior* (of about 0.05 on average) and did not change statistically significantly over time regarding the plots with an extinction and presence of this tree host. Independently from the occurrence of *F. excelsior*, resampled vegetation plots were characterized by statistically significantly higher values of almost all vegetation parameters analyzed (apart from the Shannon index), with the highest shift over time reported for CWM of reaction EIV (an increase of about 0.08 on average), and low ranges of shifts identified for remaining characteristics of vegetation (not exceeding 0.04 on average; Fig. 3 and Table 1).

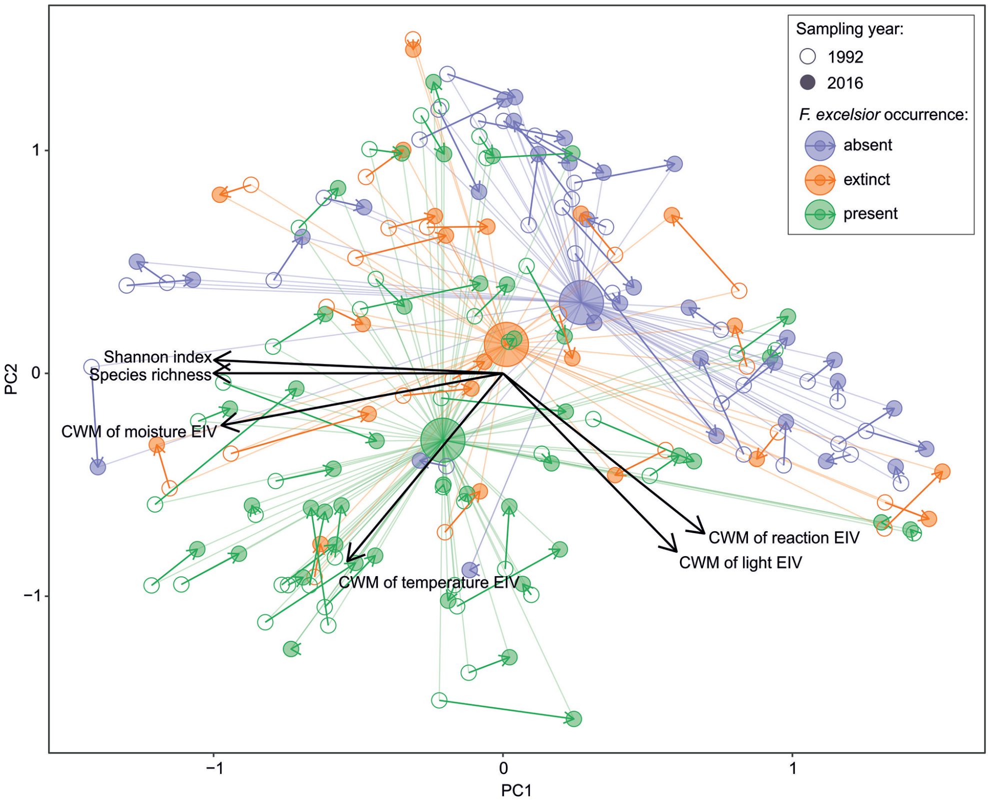

Fig. 2. Results of PCA ordination illustrating differences in species composition of epiphytic bryophytes between historical (1992) and resampled (2016) vegetation plots, and regarding the status of *F. excelsior* in plots (absent in 1992 and 2016, extinct in 2016, and present in 1992 and 2016). Points represent vegetation plots. Large circles are centroids of plots representing the status of *F. excelsior*. Thick arrows represent epiphytic bryophytes vegetation characteristics significantly ($P<0.05$) correlated with ordination results. Thin arrows indicate the direction of change in species composition over time

Abbreviations: CWM – community weighted mean; EIV – ecological indicator value.

Table 1. Parameters of mixed effect models testing for differences in epiphyte vegetation characteristics regarding the status of *F. excelsior* in plots (absent, extinct, and present), and shifts between two time periods of bryophyte vegetation sampling (1992 and 2016)

Response variable	Mixed model parameters				ANOVA			
	σ^2	SD	R^2_m	R^2_c	Predictor	X^2	df	P
Species richness	0.017	0.133	0.014	0.063	Year	4.957	1	**0.025**
					Fra.exc	20.079	2	**<0.001**
					Year : Fra.exc	3.578	2	0.167
Shannon index	0.018	0.135	0.161	0.701	Year	6.491	1	**0.011**
					Fra.exc	20.151	2	<0.001
					Year : Fra.exc	3.615	2	0.164
CWM of light EIV	0.007	0.087	0.041	0.589	Year	8.831	1	**0.002**
					Fra.exc	2.444	2	0.294
					Year : Fra.exc	0.891	2	0.640
CWM of temp. EIV	0.002	0.051	0.080	0.684	Year	5.769	1	**0.016**
					Fra.exc	7.066	2	**0.029**
					Year : Fra.exc	8.552	2	**0.014**
CWM of moisture EIV	0.012	0.141	0.126	0.878	Year	6.359	1	**0.012**
					Fra.exc	13.971	2	**<0.001**
					Year : Fra.exc	4.748	2	0.093
CWM of reaction EIV	0.151	0.389	0.027	0.911	Year	21.522	1	**<0.001**
					Fra.exc	1.501	2	0.471
					Year : Fra.exc	4.241	2	0.120

Abbreviations: CWM – community weighted mean; EIV – ecological indicator value; temp – temperature; year – sampling year; Fra.exc – *F. excelsior* status. Statistically significant results are in bold.

At the host level, species richness, Shannon index, and the contribution of bryophytes with higher substrate reaction requirements (CWM of reaction EIV) were significantly higher in 2016 than in 1992 (about 4.17, 0.09, and 0.16 on average, respectively). Values of CWMs of light, temperature, and moisture EIVs did not change significantly over time (Fig. 4).

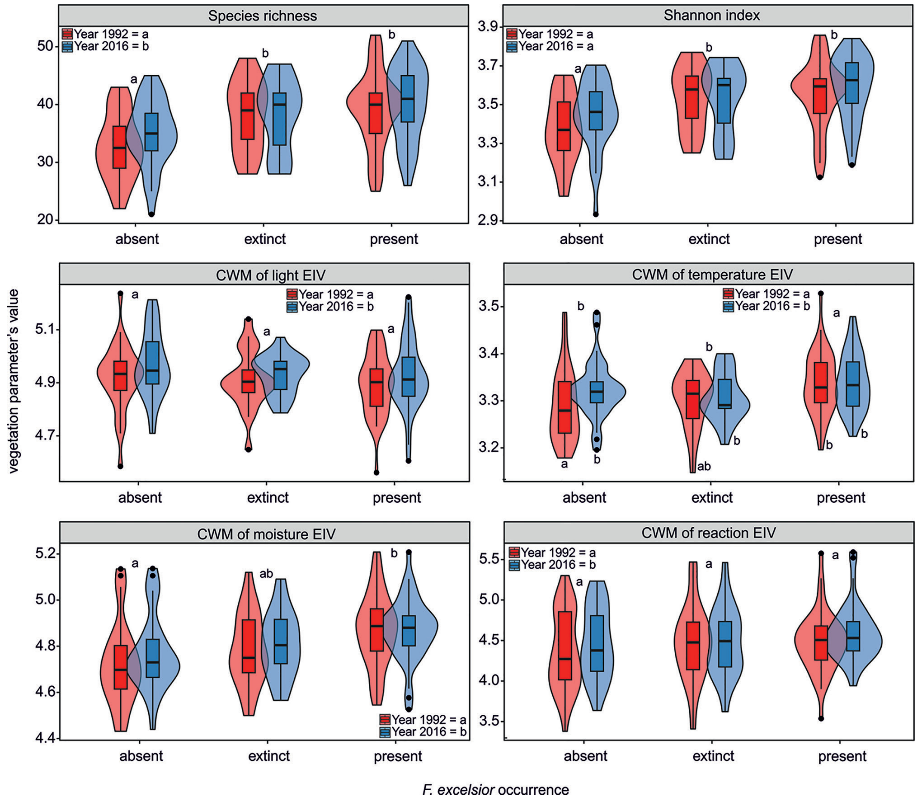

Fig. 3. Comparison of differences in epiphyte vegetation characteristics regarding the status of *F. excelsior* in plots (absent, extinct, and present), and shifts between two time periods of bryophyte vegetation sampling (1992 and 2016). Each plot shows the Kernel density plot (red and blue backgrounds) with a box-plot of the same data. Box covers the 95% confidence range. The thick horizontal line is the median. Black points are outliers. Letters show the significance of results from the post hoc Tukey's posteriori test including single effects of the year of sampling (see the legend on each graph), single effects of *F. excelsior* status (letters above the box-plots), and interaction between the year of sampling and *F. excelsior* status (letters under the boxplots; shown only if the interaction was statistically significant)

Abbreviations: CWM – community weighted mean; EIV – ecological indicator value.

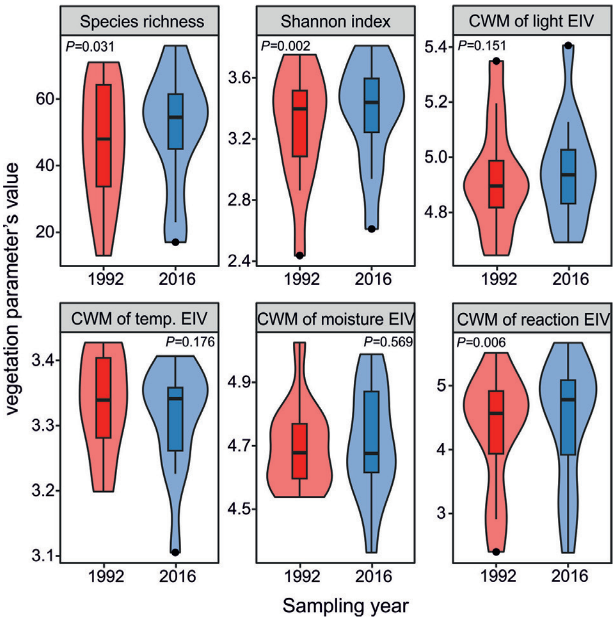

Fig. 4. Comparison of changes in community weighted mean values of ecological indicator values (EIVs), species richness, and Shannon diversity index between the two periods of epiphytic bryophytes sampling (1992 and 2016) at tree host level. Each plot shows the Kernel density plot (red and blue backgrounds) with a box-plot of the same data. Box covers the 95% confidence range. The thick horizontal line is the median. Black points are outliers. The thick horizontal line is the median

Abbreviations: CWM – community weighted mean; EIV – ecological indicator value, temp – temperature.

Based on the results of PCA ordination performed for tree hosts, we observed the multidirectional and tree species-specific shifts in species composition of epiphytes between two sampling periods (Fig. 5; Supplementary Table 1). We identified *B. pendula*, *C. avellana*, *F. excelsior*, *P. tremula*, *T. cordata*, and *U. glabra* as hosts revealing the largest, and *A. platanoides*, *C. betulus*, and *P. sylvestris* as hosts revealing the smallest ranges of shifts in bryophyte species composition over time. The gradient along the PC1 axis explained about 48% of variance variability. It ordered tree hosts along the epiphytes' temperature (CWM of temperature EIV) and reaction (CWM of reaction EIV) requirements, as well as species richness and Shannon index, identifying *C. betulus*, *F. excelsior*, *Q. robur*, and *T. cordata* as trees with the highest values of these parameters. The gradient along the PC2 axis explained about 26% of variance variability, and divided tree hosts based on the species' light and moisture demands.

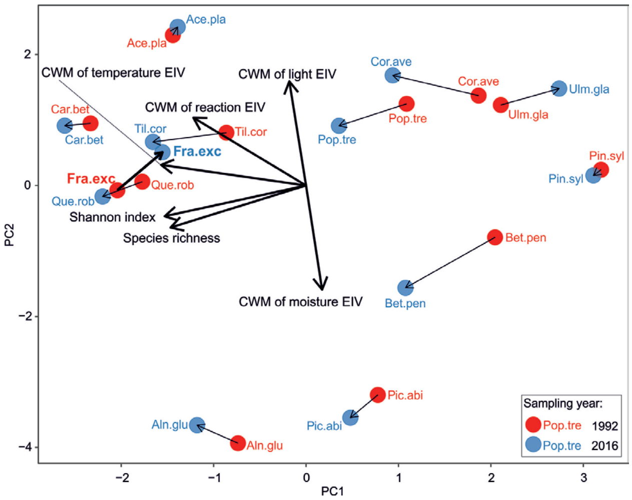

Fig. 5. Results of PCA ordination performed for the species composition of epiphytic bryophytes surveyed in 1992 and resurveyed in 2016 regarding tree host level.Red and blue labels represent tree host species names: Ace.pla – *A. platanoides*, Aln.glu – *A. glutinosa*, Bet.pen – *B. pendula*, Car.bet – *C. betulus*, Cor.ave – *C. avellana*, Fra.exc – *F. excelsior*, Pic.abi – *P. abies*, Pin.syl – *P. sylvestris*, Pop.tre – *P. tremula*, Que.rob – *Q. robur*, Sor.auc – *S. aucuparia*, Til.cor – *T. cordata*, Ulm.gla – *U. glabra*. Thick arrows represent epiphytic bryophytes vegetation characteristics significantly ($P<0.05$) correlated with ordination results. Thin arrows indicate the direction of change in species composition over time

Abbreviations: CWM – community weighted mean; EIV – ecological indicator value.

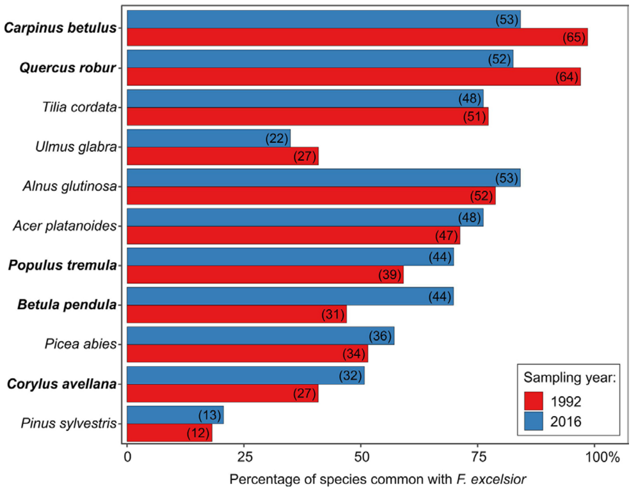

Fig. 6. Changes in percentage contribution of *F.excelsior*-inhabiting epiphyte species recorded on alternative tree hosts between historical (1992) and resurveyed (2016) data. Numbers in brackets represent the number of species recorded on alternative tree hosts, common with *F. excelsior*. Tree hosts revealing the largest shifts in the contribution of *F.excelsior*-inhabiting epiphytes are marked in bold

We found that *B. pendula*, *C. avellana*, and *P. tremula* in 2016 hosted about 23%, 10%, and 11%, respectively, more *F. excelsior*-affiliated bryophyte species than in 1992, while *C. betulus* and *Q. robur* were the trees hosting about 14% less *F. excelsior*-inhabiting epiphyte taxa recently than historically. For the remaining tree hosts, temporal shifts in the hosting of *F. excelsior*-associated bryophyte species were weak and did not exceed the difference higher than about 6% (Fig. 6).

Discussion

Patterns of species composition of *F. excelsior*-dependent bryophytes at the plot level

The invasion of *H. fraxineus* resulted in a massive decline in the population of this tree by 85% in the Białowieża Forest (Cholewińska et al., 2018). For these reasons, it was expected that *F. excelsior* dieback would decrease the richness and diversity of *F. excelsior* associated bryophytes, which may be expressed, for instance, by increasing compositional similarities of bryophytes amongst the plots. One of the most pronounced symptoms of biotic homogenization is the replacement of more specialized species by generalists (Olden et al., 2004, Řepka et al., 2015; Lososová et al., 2016; Dyderski et al, 2018; Cholewińska et al., 2020; Staude et al., 2020, Staude et al., 2022). Thus, specific interactions between species are changing and colonization by species of higher competitive abilities may be promoted (Czortek et al., 2018; Wysocki et al., 2024). However, in our study, we did not detect any symptoms of biotic homogenization, as changes in bryophyte composition over time (between 1992 and 2016) and between plots representing different statuses of *F. excelsior* presence were weak. Regardless of the sampling period, we found that the species richness of bryophytes, as well as their diversity (expressed by Shannon index) in plots containing *F. excelsior* were slightly higher than in plots without the presence of this tree but did not differ substantially compared to plots with recent extinction of *F. excelsior*. Furthermore, the bryophyte communities in the plots with *F. excelsior* contained a higher contribution of wet-demanding bryophytes than those without *F. excelsior*. This may suggest that the higher species richness and diversity of bryophytes in plots with *F. excelsior* (compared to plots without *F. excelsior* presence) could be explained more by differences in habitat conditions amongst floodplain, alder carr, and mixed deciduous forests than loss of *F. excelsior*.

The lack of more pronounced shifts in the composition of epiphytes may be explained by a high degree of bryophyte species turnover amongst host tree species composing the tree layer in plots, growing there in a high variation of ages and sizes, and thus capable of hosting a high number of *F. excelsior*-specific epiphytes. The high diversity of tree host species, in turn, may correspond to high microhabitat and microclimate heterogeneity (e.g., cracks in the bark of varying size and depth, bark irregularities, remnants of branches, scars from branches, and bark splintering). This may be confirmed by the high predictive power of plot identity as a random effect in the models, which explained more variability than fixed effects linked with the time of survey (1992 and 2016) and *F. excelsior* status in the plots. These random effects might include the mosaic structure and the high diversity of microhabitats and microclimates within plots, which could allow bryophytes to find suitable conditions for growth on trees other than *F. excelsior*. On the other hand, low rates of shifts in the composition of the epiphytic bryophyte species may be explained by the possible formation of new microhabitats after ~20 years since the first sampling was performed, which previously did not exist or were not possible to colonize by *F. excelsior*-specific bryophytes. These microhabitats may be characterized by different exposure to light and temperature, rate of water flow according to tree inclination, as well as varying pH of bark. This may explain the lack of differences in the proportion of species representing different requirements for light, temperature, as well as the bark reaction (pH), both over time and amongst the plots with varying *F. excelsior* occurrence status. Therefore, the heterogeneous tree layer composed of a high number of tree hosts may be an important factor in shaping the stability of epiphytic bryophyte communities by providing multiple opportunities to colonize alternative tree species (Łubek et al., 2020; Mitchell et al., 2021). However, apart from high availability of tree hosts and specific microhabitats and microclimates, the community assembly processes of epiphytes are shaped by their colonization abilities, linked with dispersal efficiency (Smith, 1982; Snäll et al., 2004; Löbel et al., 2006) and growth rates (Löbel & Rydin, 2009; Łubek et al., 2020; Łubek et al., 2021a; Łubek et al., 2021b).

Temporal changes in species composition of *F. excelsior*-associated bryophytes at the tree level

Trees as a substrate possess a complex of functional traits and habitat properties, i.e.: longevity, maximal dimension (place on the bark to inhabit), pH of the bark, water capacity, and bark physical complexity. In this context, trees can be compared to islands, where the appearance of individual species is linked to the development (life span) of the island (Taylor & Burns, 2015). In this case, the tree host as an 'island' changes with size, and therefore physical and chemical characteristics of the bark may become more suitable for different epiphytic bryophytes over time. Since the dynamic of epiphyte composition change is time-dependent, the longer a specific host tree persists, the more beneficial it is to the organisms that inhabit its bark (Kiebacher et al., 2017). On the other hand, the tree host 'islands' may serve as transient habitat patches in a dynamic forest ecosystem. The metapopulation concept presented by Löbel and Rydin (2009) focuses on how species persist in such dynamic ecosystems, where the survival of epiphytes depends on their dispersal strategies, and local extinctions may occur a long time after the particular host tree collapses. Examining the patterns of bryophyte species composition and diversity in the context of particular tree species hosts, we explored that rates of temporal changes in epiphyte vegetation were tree species-specific. This may be another evidence of high bryophyte species turnover over time, which corresponds to low rates of shifts in their species richness and Shannon diversity index, and slight changes in the proportion of species with different ecological demands at the plot level. This high tree host dependency allowed us to detect two different patterns of shifts in epiphyte composition over time at the level of tree hosts.

Species composition of close-to-natural forests is shaped to a high extent by insect outbreaks (*sensu* Veblen, 1992) or catastrophic windthrows (Fischer & Fischer, 2009), which affect the formation of gaps with the natural regeneration of trees (Bobiec et al., 2000). However, gaps in the canopy can also be the consequence of invasions by nonnative *H. fraxineus* infesting *F. excelsior*. The first pattern concerned light-demanding pioneer tree and shrub species (i.e. *B. pendula*, *P. tremula*, and *C. avellana*), which, due to their fast growth (Myking et al., 2011), can first colonize newly established gaps in tree canopy, and develop rapidly features important for colonizing their bark by epiphytic species (Ihlen et al., 2001; Wierzcholska et al., 2024). Thus, following the mass-ratio hypothesis (Kershaw & Mallik, 2013), the development of specific microhabitats on light-demanding pioneer trees and shrubs in gaps to a large extent may influence the ecosystem functions through, *inter alia*, shaping the patterns of bryophytes species composition. Alongside increasing the diameter at breast height and age of trees, numerous structural cracks in the cortex start to develop in tree bark (Larrieu et al., 2018), as well as the water-holding capacity and pH of the bark increase (Barkman, 1958). These physico-chemical characteristics of the bark could promote the colonization of trees not only by pioneer bryophytes but species representing more advanced stages of epiphyte assemblages succession (Gustafsson & Eriksson, 1995). Thus, bryophytes occurring previously on *F. excelsior* could begin to colonizing these light-demanding pioneer trees as the abiotic conditions could become more suitable for them over time, leading to recently higher species richness and Shannon diversity index, along with a slight increase in the contribution of light-demanding species both at plot and the level of tree species hosts. This may also explain the fact that some species with relatively high light demands, such as *Dicranum viride* (listed in Annex II of the European Habitats Directive; EEC, 1992), which ~20 years ago was not recorded, has recently been able to colonize living trees (Stebel et al., 2015; Wysocki et al., 2023). Therefore, gaps in the canopy can promote the spread of functionally unique species, often considered threatened. In this light, our results are consistent with those that were found by Mitchell et al. (2014) – a unique study which investigated the impact of *F. excelsior* dieback on bryophytes. The abovementioned authors reported that the pioneer woody species *Salix caprea* was one of the best alternative hosts of *F. excelsior*-affiliated bryophytes.

The second pattern referred to tree host species that revealed a slight loss of *F.excelsior* inhabiting epiphytes, i.e. *C. betulus*, *T. cordata*, and *Q. robur*, which may be explained, *inter alia*, by the maturation of the tree stands. Thus, changes in tree stand structure could result in increasing the compositional similarities of bryophyte assemblages inhabiting, for instance, *T. cordata* and *F. excelsior* in 2016, as well as those occurring on *Q. robur* in 2016 compared to *F. excelsior* in 1992. The crowns of these trees cause greater shading than in the case of *F. excelsior* trees with loose crowns, which may result in a slightly lower number of *F. excelsior*-affiliated species recorded on *C. betulus* and *Q. robur* recently. By analyzing the changes in bryophyte composition over time, *C. betulus* and *Q. robur* could be overgrown by more competitive (than in the case of *F. excelsior*-affiliated species) bryophytes of higher temperature demands, and higher requirements for the bark reaction (higher bark pH), which, in turn, could be characterized by higher competition abilities. Similar patterns were demonstrated in managed old-growth forests of various land-use and disturbance history in northern Europe and northern America. In these studies, a significant correlation was found regarding the tree stand maturation and the bryophyte species inhabiting their bark. These researches showed that old trees support a distinct pool of epiphytic bryophyte specialists of higher requirements for bark reaction (McGee and Kimmerer 2002; Edman et al., 2016).

Conclusions

Despite the drastic reduction in the number of *F. excelsior* trees in the Białowieża Forest, the high diversity of *F. excelsior*-associated epiphytic bryophytes was maintained due to the high diversity of alternative tree hosts. Other trees can ensure the long-term persistence of *F. excelsior*-associated bryophytes, which could be able to exploit other niches than those offered by *F. excelsior* in the microhabitat-heterogeneous primeval forest ecosystem. Early successional *B. pendula* and *P. tremula* were more suitable for acquiring bryophytes from *F. excelsior*, compared to late successional *C. betulus* and *Q. robur*. Therefore, factors shaping the diversity of epiphytes at the scale of tree host species could exert strong impacts on the compositional dynamics of epiphyte assemblages at the plot level scale. Our results may hint at the high resilience of the Białowieża Primeval Forest, expressed by wide abilities to mitigate the invasion-driven effects on the diversity of epiphytic bryophytes.

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Conflict of interest

The authors declare no conflict of interest.

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