



Invasive *Prunus cerasifera* alters understory diversity in the early successional oak-hornbeam forests

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Abstract The number of naturalizing non-native species continues to increase in the Anthropocene, with numerous species becoming invasive even after prolonged lag phases. A notably overlooked group among invasive trees and shrubs is the Rosaceae family, with *Prunus cerasifera* emerging as one of the species whose effects on forest ecosystems remain poorly understood despite its wide occurrence across the introduced range. We aimed to evaluate how the invasion of *P. cerasifera* affects the taxonomical, functional, and phylogenetic diversity of the understory of the early successional stages of oak-hornbeam forests. Using the *P. cerasifera* invasion gradient, defined as increasing cover of this invasive tree, and implementing the ordination and linear regression methods, we found the prominent effects of *P. cerasifera* on all three examined metrics of plant species diversity. We revealed that increasing the cover of *P. cerasifera* not only increased species richness

but also altered the phylogenetic structure of the understory by introducing new clades. Additionally, it influenced community assembly processes by reducing the importance of habitat filtering and strengthening the role of interspecific competition in shaping the community structure. Our study presents the first assessment of *P. cerasifera*'s impact on understory diversity along its invasion gradient, enabling a comprehensive evaluation of invasion-driven effects on the functioning of forest ecosystems during the early stages of succession. Our findings are not only essential for formulating effective management and conservation strategies but also critical for guiding how invasive tree species can influence the trajectories and mechanisms of the secondary forest succession.

Keywords Cherry plum · Community assembly rules · Herb layer vegetation · Non-native tree effects · Phylogenetic diversity · Secondary forests

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Introduction

Among invasive species, trees and shrubs are especially important due to their longevity and ability to transform ecosystems as foundational species (Ellison et al. 2005; Corenblit et al. 2014; Roy et al. 2024). By various growth rates and canopy characteristics, they provide species-specific modifications to resource availability and dependent biota (von Arx et al. 2012; Aerts et al. 2017; Nyssen et al. 2024). That way,

invasive tree and shrub species not only affect biodiversity (Brundu et al. 2020; Wohlgemuth et al. 2022; Vilà et al. 2024), but also forest functioning and ecosystem services (Castro-Díez et al. 2014; Lázaro-Lobo et al. 2025).

The impacts of invasive tree species on understory species diversity have been extensively studied for years. A recent review of the impacts of the most widespread invasive tree species in Europe (Wohlgemuth et al. 2022) revealed 720 cases of comparing native and invasive stands for vascular plant diversity. However, 73.8% of these cases revealed no significant differences and were limited to seven tree species. Vilà et al. (2024) concluded that one-third of 4259 field studies on 104 invasive plant species in Europe focused on just five species, among them only one tree species (*Robinia pseudoacacia*). Therefore, impacts on numerous invasive tree species are still insufficiently recognized (Carboneras et al. 2018; Roy et al. 2024).

Despite the growing interest in integrating both functional and phylogenetic diversity metrics into recent studies on vegetation ecology (e.g. Czortek et al. 2021, 2023; Dyderski and Jagodziński 2021; Nicod and Gillet 2021; Bury et al. 2024; Anibaba et al. 2025), only a few approaches, to date, assessed the impacts of invasive trees and shrubs on forest understory in the context of effects on the community assembly processes (e.g. Chabrierie et al. 2010; Terwei et al. 2016; Sitzia et al. 2018; Fernandez et al. 2021; Henry et al. 2021; Larsen et al. 2024; Bury et al. 2024) or the species' evolutionary relatedness structure (e.g. Piwczyński et al. 2016; Livingstone et al. 2020; Dyderski and Jagodziński 2021). This predominant focus on the invasion-driven effects on taxonomic diversity and species composition (see review in Dyderski and Jagodziński 2021) led to a strong site-specificity and context-dependency of the obtained patterns, significantly limiting their applicability to similar ecosystem types across various geographical regions (Olden et al. 2018). For instance, some researchers assessing the impacts of *Prunus serotina* on forest ecosystems revealed all types of invasion-driven responses of herb layer species composition: positive (e.g. Dyderski and Jagodziński 2021; Bury et al. 2024; Bury and Dyderski under review), no effect (e.g. Chabrierie et al. 2010), or negative (e.g. Godefroid et al. 2005; Halarewicz and Żołniercz 2014; Gentili et al. 2019). Therefore,

simultaneous assessment of the three biodiversity facets may allow for obtaining more universal patterns of invasion-driven effects on the functioning of ecosystems (Dyderski and Jagodziński 2021; Czortek 2023; Larsen et al. 2024). Moreover, this approach may be used not only as a predictor of ecosystem functions but a measure of the ecosystem invasibility, conservation status, recovery or restoration effectiveness, as well as a tool for effective formulation of conservation priorities and invasive species management strategies (Blackburn et al. 2011; Aerts et al. 2017; Novoa et al. 2020).

The pool of naturalizing non-native species is still increasing (Seebens et al. 2017), and new species become invasive, especially after a long lag time (Kowarik 1995). A good example of an underrecognized group of invasive tree species is the Rosaceae family. According to the global list of invasive trees and shrubs (Rejmánek and Richardson 2013), among 751 taxa, 92 belong to this family, while most of them are insufficiently recognized, with few exceptions (e.g. *P. serotina*; Engel et al. 2024). These species were massively introduced due to ornamental and food production functions, and many of them produce fleshy fruits, attracting dispersers (Pairen et al. 2006; Wróbel et al. 2021; Kurek et al. 2024). One example of a non-native tree representing this group is the cherry plum *P. cerasifera* Ehrh. (= *P. divaricata* Ledeb., *P. myrobalana* (L.) Desf.), native to southeastern Europe, as well as southwestern and central Asia (Weber 2017; POWO 2022). Owing to its high ecological plasticity (Popescu and Caudullo 2016; Chytrý et al. 2018), *P. cerasifera* can successively invade both non-forest and forest ecosystems across a wide range of human-driven transformation levels and successional stages (Adamowski et al. 2002; Adamowski and Wołkowycski 2014), including ecosystems of the highest conservation values, such as the Białowieża Primeval Forest (Czortek et al. 2024).

Although *P. cerasifera* is widely recognized by the public and classified as a non-native, naturalized, or invasive species across northwestern Africa, western and eastern North America, southwestern South America, New Zealand (Weber 2017; POWO 2022), and Europe (Popescu and Caudullo 2016; Dobrzycka-Kraheil and Medina-Villar 2020), its impact on the understory vegetation of forest ecosystems remains unexplored (Czortek et al. 2024). A comprehensive assessment of the effects of *P. cerasifera* invasion,

especially during the early stages of forest succession, is particularly crucial for developing effective management strategies aimed at understanding its impacts on biodiversity, community assembly, trophic interactions, biogeochemical processes, ecosystem functioning, and successional trajectories (Blackburn et al. 2011; Aerts et al. 2017). Therefore, we aimed to assess the impact of invasive *P. cerasifera* on the understory vegetation of early successional stages of oak-hornbeam forests. We hypothesized that *P. cerasifera* will influence not only the species composition and taxonomic diversity but also alter community assembly processes and the evolutionary relatedness structure of plant species, as reflected in the effects on the functional and phylogenetic diversity of the understory.

Quantifying the intensity of invasive species impacts requires rigorous methodology (Kumschick et al. 2015; Barney et al. 2015; Bury et al. 2024). One such method involves assessing the *per capita* effects of an increasing invader's abundance on particular components of vegetation diversity. *Per capita* effects are considered a reliable tool for comparing the impacts of invasive plants across different ecosystems, increasing the predictive strength of the observed patterns (Parker et al. 1999; Kumschick et al. 2015). Thereby, to investigate the *per capita* impacts of *P. cerasifera* on the understory, we established an invasion gradient, allowing the effects on plant species diversity to be directly linked to the increasing cover of *P. cerasifera* in the canopy layer.

Materials and methods

Study area

We conducted our study in the northern part of the Białowieża Clearing, located between the Białowieża village—the largest settlement within the Polish part of the Białowieża Primeval Forest—and the Białowieża National Park (Fig. 1). This area experienced continuous agricultural use from the seventeenth century until the second half of the twentieth century, with a cessation of agricultural activities markedly accelerating after 1989. Currently, the northern part of the study site forms a mosaic landscape composed mostly of abandoned agricultural fields, mesic meadows, and pastures. This

area also includes early successional stages of oak-hornbeam forests (*Tilio-Carpinetum*), not older than approximately 30–40 years, and composed of *Betula pendula*, *Populus tremula*, *Salix caprea*, *Carpinus betulus*, *Quercus robur*, *Tilia cordata*, naturalized *Malus domestica* and *Pyrus communis*, as well as *P. cerasifera*.

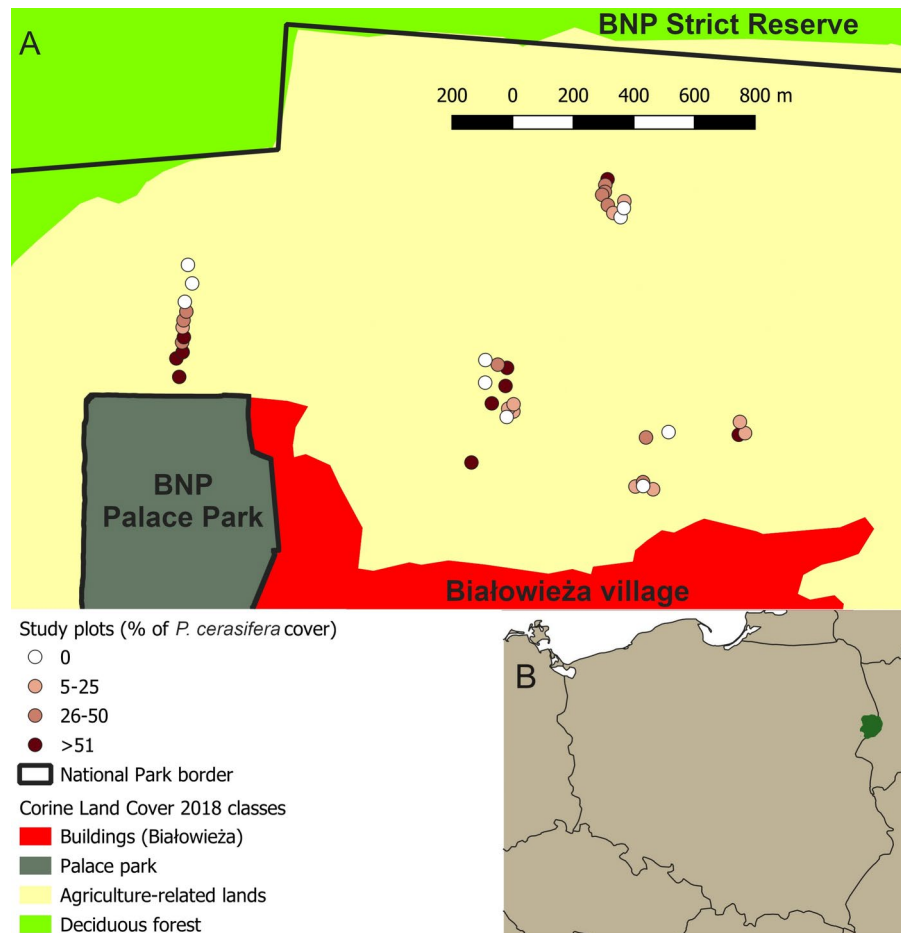
Results of long-term study on secondary succession in the Białowieża Clearing (Adamowski and Bomanowska 2011) confirm that undisturbed secondary succession on abandoned agricultural areas leads from a typical segetal communities composed of non-native weeds, through mesic meadow-like vegetation, to the formation of a juvenile stand up to 20 m in height, with an understory composed exclusively of native plant species. The presence and dominance of native trees after 36 years of succession show that, despite approximately 350 years of agricultural use, habitat conditions allow the return of oak-hornbeam forest. The shrub layer developed in the 11th year of observations, and the tree layer in the 13th year. Canopy cover reached 50% in the 21st year of observations. Several forest indicator herb species were observed: *Convallaria majalis* from year 26, *Anemone nemorosa* from year 29, and *Isopyrum thalictroides* and *Carex digitata* from year 34 of secondary succession (Adamowski and Bomanowska 2011).

Historical records reveal that *P. cerasifera* was introduced in the Belarusian part of the Białowieża Primeval Forest by the 1960s (Smirnov 1965). The first confirmed reports of this non-native tree on the Białowieża Clearing are from the late 1970s, as documented in herbarium specimens collected by the Białowieża Geobotanical Station. Recently, this non-native tree has become relatively common in most patches of abandoned non-forest vegetation and early successional oak-hornbeam forests developing on the Białowieża Clearing. It may occur there as scattered individuals, as an admixture in the canopy, or locally dominate both the shrub and tree layers, reaching canopy cover up to 90%.

Vegetation survey

We conducted our study in 2023 on 40 vegetation plots (25 m² each) with understories predominantly composed of native plant species and negligible contributions from non-native weeds, representing relicts of the study area's historical agricultural use

Fig. 1 Study area with four study sites representing early successional stages of oak-hornbeam forest, located on the Białowieża Clearing in the surrounding of the Strict Reserve of the Białowieża National Park



(i.e., *Lamium purpureum*, *Myosotis arvensis*, *Sonchus oleraceus*, *Vicia sativa* subsp. *nigra*, *V. hirsuta*, and *V. tetrasperma*), invasive species (i.e. *Solidago canadensis*) or other non-native kenophytes (i.e. *Erigeron annuus* and *Oxalis corniculata*). Due to the irregular occurrence of *P. cerasifera* in the Białowieża Clearing, we set up vegetation plots in four blocks of patches representing the early successional stages of oak-hornbeam forest (Fig. 1). To stratify the distribution of vegetation plots in the study area we established them in four classes of *P. cerasifera* cover in the canopy layer: ten without *P. cerasifera*, ten with *P. cerasifera* cover of 5–25%, ten with 26–50% cover, and ten with > 50% cover. To assess the effects of *P. cerasifera* along the invasion gradient described above, we subsequently used its cover values as a continuous explanatory variable in the analyses. To minimize the potential influence of other trees on the understory species composition, we

selected vegetation patches in which *P. cerasifera* was the predominant species composing the canopy, with the total cover of native (i.e. *P. tremula*, *Q. robur*, and *T. cordata*) and other non-native tree species (i.e. *M. domestica*, and *P. communis*) in the stand not exceeding 5% (Online Resource 1). To include both the spring and summer phenophases of the understory, we surveyed vegetation in June, which corresponds to the last month of spring in the northern hemisphere. Within each plot, we recorded vascular plant species and their percentage cover in nine-degree Braun-Blanquet scale ($r < 0.01\%$, $+ - 0.1-1\%$, $1-1.1-3\%$, $2-3.1-5\%$, $2a-6-15\%$, $2b-16-25\%$, $3-26-50\%$, $4-51-75\%$, and $5 > 75\%$ cover), converted then to the van der Maarel scale (Online Resource 2 Nomenclature of plant species follows Euro+Med checklist (<http://www2.bgbm.org/EuroPlusMed/>, accessed 17 Mar 2025)). We excluded from the analyses tree and shrub seedlings, and focused solely on herbaceous

plant species. Following Gilliam and Roberts (2003), herbaceous plants are better indicators of habitat conditions, disturbance, and potential future succession pathways than trees and shrubs, as they respond to environmental changes more rapidly. Moreover, values of functional traits in databases usually reflect adult trees, not matching conditions occurring in the understory layer.

Understory diversity characteristics

To account for the taxonomic diversity of the understory, for each plot, we calculated plant species richness and Shannon's index (Online Resource 2). To focus on the species' relatedness structure based on their phylogenesis and evolutionary trajectories, we computed the Faith's phylogenetic diversity index for each plot using the *PhyloMeasures* package (Tsirogianis and Sandel 2016), based on a phylogenetic tree acquired using the *V.PhyloMaker* package (Jin and Qian 2022; Online Resource 2). This index sums the branch lengths of the phylogenetic tree that correspond to all species present in the community. Negative values of this index suggest distinctive phylogenetic clustering, indicating that species from specific clades occur more frequently than would be expected by chance (Tsirogianis and Sandel 2016; Nicod and Gillet 2021; Czortek 2023).

To assess the functional composition of the understory vegetation, for each plot, we compiled data on eight plant functional traits from the LEDA (Kleyer et al. 2008), BIEN (Maitner et al. 2018), BioFlor (Klotz et al. 2002), and Pladias (Chytrý et al. 2021) databases. Traits describing the leaf economic spectrum, such as specific leaf area [$\text{cm}^2 \text{g}^{-1}$] and leaf dry matter content [mg g^{-1}], along with plant size characteristics, including canopy height [m] and life form (categorical trait), act as indicators of species' competitive abilities. These traits provide insights into strategies for resource acquisition, allocation, and distribution across different plant organs. Traits related to dispersal and reproductive biology, such as seed mass [mg], the onset and duration of flowering [months], and pollination mechanisms (insect, wind, or self-pollination) provide data on reproductive strategies, seed dispersal distances, survival adaptations, and plant responses to habitat filters (Westoby 1998; Grime 2006; Díaz et al. 2016).

To determine the species' ecological preferences, we used the ecological indicator values (EIV) for light (EIV-L), temperature (EIV-T), moisture (EIV-M), soil reaction (EIV-R), and soil fertility (EIV-N; Ellenberg and Leuschner 2010). EIVs, established by vegetation ecologists, are commonly applied to infer species' ecological niches in the absence of direct instrumental measurements (e.g., Evangelista et al. 2016; Czortek et al. 2018; Ridding et al. 2020). Although EIVs have limitations due to their categorical nature and reliance on expert judgment (Schaffers and Sýkora 2000), comparative analyses with empirical measurements have demonstrated their reliability in characterizing species' ecological requirements (Dzwonko 2001; Szymura et al. 2014).

Data on functional traits and EIVs were incomplete for part of the recorded species (Table 1). However, rather than excluding these species from the analyses, we employed a phylogenetic imputation approach to estimate the missing values. To achieve this, we constructed a phylogenetic tree incorporating all plant species identified in the study plots, utilizing a phylogenetic megatree framework implemented in the *V.Phylo.maker* package (Jin and Qian 2022; Online Resource 2). The constructed phylogenetic tree, along with available functional trait data, EIVs, and phylogenetic eigenvectors (provided using the PVR package; Diniz-Filho et al. 1998; Santos 2025; Online Resource 2), was used to conduct a random forest-based imputation of missing values. This imputation procedure was implemented through the *missForest* package (Stekhoven and Bühlmann 2012), following the approach designed by Penone et al. (2014). The first 15 phylogenetic eigenvectors explained 73.12% of the variation in phylogenetic distances between species. The normalized root mean squared error for the imputed continuous traits and the misclassification rate for categorical traits were both somewhat low (0.31 and 0.28, respectively; Online Resource 2). Inspecting these results, and comparing the numerical functional traits distribution between the imputed and original dataset (Online Resource 3), we concluded that the overall performance of the phylogenetic imputation was sufficiently reliable. Using the imputed trait data, we then calculated the community-weighted mean values (CWM; weighted by species abundance; Violle et al. 2015) for plant functional traits and EIVs for each plot (Online Resource 2).

Table 1 Traits used in the study, their ranges, standard deviation (SD), and completeness

Numeric traits	Min	Max	Mean	SD	Completeness [%]
Flowering beginning [months]	3.000	8.000	5.509	0.961	93.442
Flowering duration [months]	2.000	8.000	3.684	1.228	93.442
Canopy height [m]	0.100	10.000	1.230	1.295	94.262
Seed mass [mg]	0.017	468.017	6.208	44.197	91.803
Leaf dry matter content [mg g ⁻¹]	114.700	392.600	224.800	65.774	86.885
Specific leaf area [cm ² g ⁻¹]	49.840	491.190	259.150	77.753	90.983
Light EIV	3.000	9.000	6.809	1.123	94.262
Temperature EIV	2.000	7.000	5.408	1.008	62.295
Moisture EIV	2.000	10.000	5.343	1.438	83.606
Soil fertility EIV	1.000	9.000	5.202	2.025	85.245
Soil reaction EIV	2.000	9.000	6.200	1.611	57.377
Categorical traits	Number of classes	Classes and their frequency			Completeness [%]
Life form	8	Chamaephytes (0.819%), Geophytes (5.737%), Hemicryptophytes (72.131%), Lianas (7.377%), Phanerophytes (1.639%), Therophytes (6.557%)			93.441
Pollination mode—insect	2	Yes (69.672%), no (21.311%)			90.983
Pollination mode—self	2	Yes (46.721%), no (44.262%)			90.983
Pollination mode—wind	2	Yes (24.590%), no (66.393%)			90.983

To evaluate the role of primary ecological mechanisms in influencing species composition and community assembly (Götzenberger et al. 2012; HilleRisLambers et al. 2012; Mudrák et al. 2019), we computed four functional diversity metrics for each plot using the *FD* package (Laliberté and Legendre 2010; Online Resource 2). Functional richness measures the range of plant functional types in a community, as well as how plants with different traits occupy the available niche space (referred to as the filled niche space; Villéger et al. 2008). Functional evenness reflects the degree of homogeneity of trait distribution within the filled niche space (Mason et al. 2005; Mouchet et al. 2010). Functional dispersion and functional divergence both assess the average dissimilarities between the trait combinations of species within the filled niche space. Functional dispersion evaluates these dissimilarities to the centroid of the filled niche space, while functional divergence quantifies the average dissimilarities of species' traits from the central point of the filled niche space. Therefore, functional divergence is more responsive to species with extreme trait values, while functional dispersion is less affected by them (Mason et al. 2005; Villéger

et al. 2008; Pla et al. 2011). Low values of functional diversity metrics may indicate the prominent role of habitat filtering or intense interspecific competition, while high values may suggest that niche differentiation plays a substantial role in shaping the community assembly rules (Chesson 2000; Mayfield and Levine 2010; Carroll et al. 2011; Cadotte et al. 2011; Spasojevic and Suding 2012).

Because Faith's phylogenetic diversity index and functional diversity metrics are inherently influenced by species richness, we calculated their standardized effect sizes (SES) to remove the confounding effect of species richness on these metrics of plant species diversity. We calculated SES accounting for the deviation of the observed metrics' values from the null models (Czortek et al. 2021). To build the null models, we used randomized community data matrices generated through the independent swap algorithm, which preserves species occurrence frequencies and sample species richness. The SESs were computed according to the code presented in Online Resource 2. Very high or very low SESs values suggest that the observed values deviate prominently from what would be expected by chance, based on the null model for a given species richness.

Statistical analyses

We conducted all statistical analyses employing R 4.3.1 software (R Core Team 2025). All R scripts with appropriate datasets used to conduct statistical analyses are presented in Online Resource 2. To evaluate the effect of *P. cerasifera* invasion on understory species composition, we conducted a Canonical Correspondence Analysis (CCA) with *P. cerasifera* cover in the tree layer as a predictor variable using the *vegan::cca()* function (Oksanen et al. 2025). Initial CCA based on raw abundance data yielded patterns that were difficult to interpret in a meaningful ecological context. To improve interpretability, we transformed the understory species composition matrix into a binary presence-absence format using the *vegan::decostand()* function (Oksanen et al. 2025), prior to conducting the final CCA. We tested the statistical significance of this influence by the PERMANOVA analysis implemented in the *vegan::anova.cca()* function (Oksanen et al. 2025).

To assess individual responses of plant species to *P. cerasifera* invasion we conducted the threshold indicator taxa analysis, implemented in the *TITAN2* package (Baker et al. 2023), using species with at least three occurrences. This analysis allowed us to determine positive and negative indicator species for *P. cerasifera* cover, as well as to assess individual species changing points, where they start decreasing their abundance. To maximise the robustness of the analysis we showed the species with reliability > 0.95. Reliability is a statistic quantifying whether the magnitude of change remains stable over a set of 500 permutations.

To investigate how the invasion of *P. cerasifera* influences the plant species diversity of the understory, as well as the CWMs of plant functional traits and EIVs in the study plots (Table 2), we built one mixed-effects model for each vegetation characteristic using the *glmmTMB::glmmTMB()* function (Brooks et al. 2017). In each model, we included *P. cerasifera* cover as a fixed effect and the site identity as a random intercept, to account for the influence of the vegetation survey design, local differences in abiotic habitat properties, and land-use history. We applied a generalized mixed-effects model with a Poisson distribution to model species richness, selecting this approach due to the relatively low dispersion parameter value (0.77; $P=0.36$) indicated by the dispersion

test result from the *DHARMa::testDispersion()* function (Hartig 2025). To examine the influence of *P. cerasifera* invasion on the Shannon's index, SES of Faith's phylogenetic diversity index, SESs of four metrics of functional diversity, and CWMs of four plant functional traits and five EIVs, we constructed 15 linear mixed-effects models (one model per one vegetation characteristic), assuming that the response variables followed a close-to-normal distribution. Initial visualization of a model for Faith's index of phylogenetic diversity revealed that some observations would be identified as influential. Using the *car::outlierTest* (Fox et al. 2024) we inspected this model for outliers and identified three observations as statistically significantly influencing its results, which allowed us to exclude them from analyses (i.e. plot G07_3: $rstudent=4.31$, $P<0.001$; plot G17_3: $rstudent=3.36$, $P=0.001$, and plot G30_2: $rstudent=3.39$, $P=0.001$, respectively; Online Resource 2. We employed the *ggeffects::ggpredict()* function (Lüdtke 2018) to examine the marginal responses of the understory vegetation characteristics to *P. cerasifera* invasion, enabling an evaluation of effect sizes and the biological relevance of the observed patterns, apart from entirely focusing on traditional statistical significance tests (Nakagawa and Cuthill 2007; Wasserstein and Lazar 2016).

Results

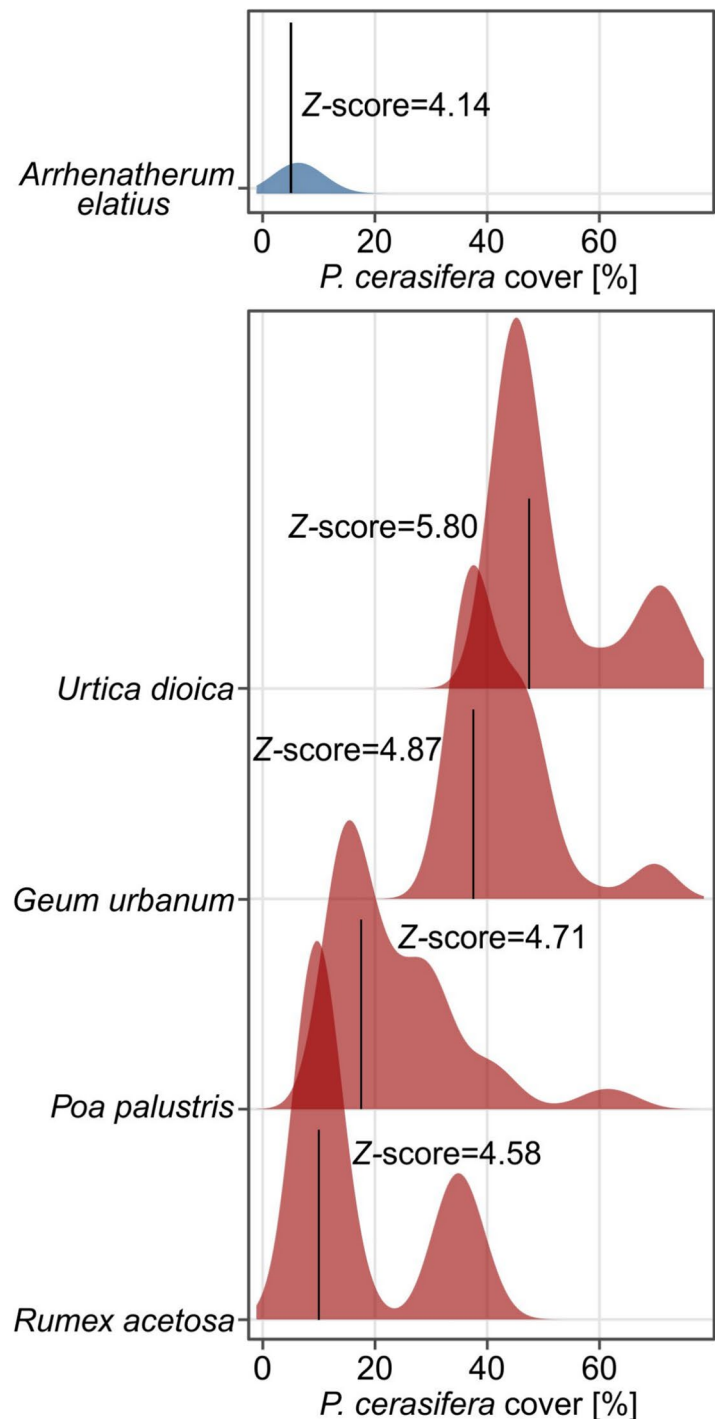
Based on the CCA ordination result, we identified a prominent influence of *P. cerasifera* cover in the tree layer on the understory species composition of vegetation plots, as reflected in their distribution along the CCA1 axis (Fig. 2). This effect was further confirmed by the PERMANOVA analysis ($\chi^2=0.104$; $F=1.400$; $P=0.013$). Most plant species demonstrated a strong association with plots characterized by low *P. cerasifera* cover, including ruderal tall herbs (e.g., *Cirsium arvense*, *Pastinaca sativa*, *Sonchus oleraceus*, *Tanacetum vulgare*, or *Verbascum nigrum*) and species typical of mesic meadows (e.g., *Argentina anserina*, *Arrhenatherum elatius*, *Achillea millefolium*, *Ranunculus acris*, or *Stellaria graminea*), both positioned on the right side of the gradient along the CCA1 axis (Fig. 2). In contrast, only a limited number of species displayed a strong affinity for plots with high *P. cerasifera* cover, belonging to the group of

Table 2 Descriptive statistics of variables used in this study

Variable	Min	Mean	Max	SD
<i>Taxonomical diversity</i>				
Species richness	19.00	29.95	42.00	5.96
Shannon's index	1.35	2.14	2.72	0.34
<i>Functional diversity</i>				
Functional richness SES	-1.02	0.75	2.63	0.79
Functional dispersion SES	-1.28	0.14	1.80	0.83
Functional divergence SES	-2.34	-0.06	1.37	0.86
Functional evenness SES	-2.37	-0.08	1.66	0.96
<i>Phylogenetic diversity</i>				
Faith's index	-2.67	-1.59	1.62	0.74
<i>CWMs of plants' functional traits</i>				
Canopy height CWM [m]	1.01	1.26	1.59	0.15
Leaf dry matter content CWM [mg g ⁻¹]	209.40	271.40	306.40	20.26
Specific leaf area CWM [cm ² g ⁻¹]	234.50	289.90	327.90	20.54
Seed mass CWM [mg]	0.82	1.54	2.44	0.46
<i>CWMs of ecological indicator values</i>				
CWM of light EIV	5.83	6.96	7.77	0.42
CWM of temperature EIV	5.15	5.44	5.65	0.15
CWM of soil moisture EIV	4.54	5.49	6.01	0.34
CWM of soil fertility EIV	4.68	6.08	7.37	0.57
CWM of soil reaction EIV	6.01	6.38	6.78	0.22
<i>P. cerasifera</i> cover [%]	0.00	30.88	90.00	28.66
Study site identity (total = 40 plots)	S1 (n = 11)	S2 (n = 11)	S3 (n = 9)	S4 (n = 9)

Min minimal value, *Max* maximal value, *SD* standard deviation, *SES* standardized effect size, *CWM* community weighted mean, *EIV* ecological indicator value

Fig. 3 Result of the threshold indicator taxa analysis (TITAN) of plant species responses to *P. cerasifera* percentage cover showing the density estimator of their abundance along the *P. cerasifera* cover gradient. Black bars denote change points for decreasing (blue) or increasing (dark red) abundance along the *P. cerasifera* cover gradient



metric of phylogenetic diversity, showing an increase from -1.86 at 0% to -1.55 at 90% of *P. cerasifera* cover in the tree layer (Fig. 4c), with 7% of the variance explained by fixed effect, and no influence of random effect (Table 3). While functional richness

and functional divergence SESs decreased slightly (from 0.84 to 0.59 and from 0.13 to -0.46 , respectively; Fig. 4d and e), functional dispersion SES increased notably (from -0.26 to 0.90; Fig. 4f) with an increase in *P. cerasifera* cover from 0 to 90%.

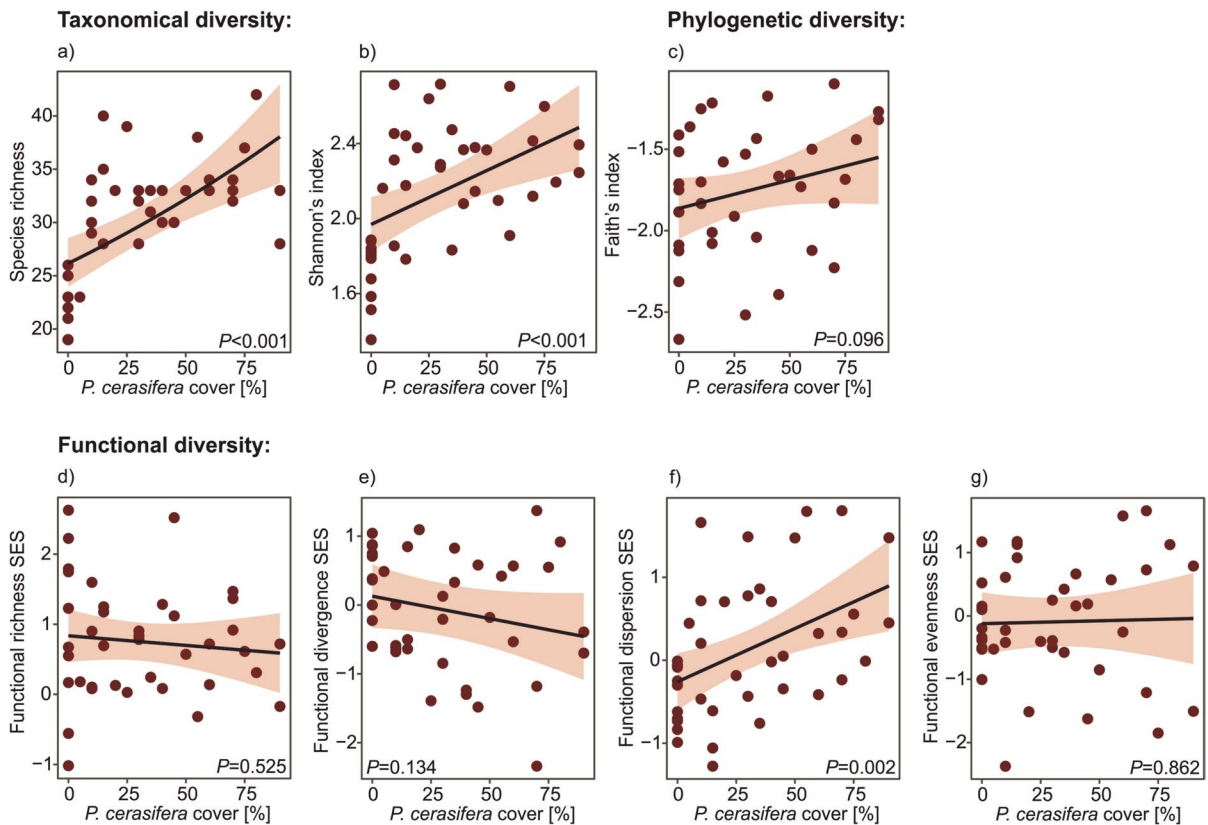


Fig. 4 Visualisation of mixed effect models testing for effects of *P. cerasifera* percentage cover on plant species' taxonomical (a and b), phylogenetic (c), and functional diversity (d–g) metrics

Taking into account functional richness SES, both random and fixed effects were responsible for only about 3% and 1% of the variability, respectively. In contrast, in the case of functional divergence SES, the random effect contributed to 12% of the variance, and the fixed effect explained only about 5% of the variability. *P. cerasifera* invasion explained about 20% of the variance in functional dispersion SES, with negligible influence of a random effect; (Table 3). We did not find effects of *P. cerasifera* cover on functional evenness SES (Fig. 4g; Table 3).

From four analysed CWMs of plant functional traits (Fig. 5a–d), only CWM of leaf dry matter content decreased noticeably in response to *P. cerasifera* cover from 279.55 mg g⁻¹ at 0% to 256.90 mg g⁻¹ at 90% (Fig. 5a), with about 13% and 12% of the variance explained by fixed and random effects, respectively (Table 3). We identified the considerable impacts of *P. cerasifera* cover on all CWMs of EIVs investigated (Fig. 5e–i). In dominance of studied

species in the tree layer, the contribution of more light-demanding species (CWM of light EIV; Fig. 5e) and plants of higher temperature requirements (CWM of temperature EIV; Fig. 5f) decreased substantially from 7.11 to 6.63 and from 5.49 to 5.34 at *P. cerasifera* cover ranging from 0 to 90%, respectively. For the CWM of light EIV, about 13% of the variance was explained by *P. cerasifera* cover, while about 35% of the variability was attributed to the study site identity. We did not detect any impact of the random factor on the CWM of temperature EIV (Table 3). Increasing the cover of *P. cerasifera* (ranging from 0 to 90% in tree layer) exerted strong positive effects on the proportion of more wet-demanding plants (an increase in soil moisture EIV CWM from 5.39 to 5.71; Fig. 5g), as well as species of higher soil fertility (an increase in soil fertility EIV CWM from 5.90 to 6.42; Fig. 5h) and reaction requirements (an increase in soil reaction EIV CWM from 6.28 to 6.57; Fig. 5i). Regarding CWMs of soil moisture and soil fertility CWMs,

Table 3 Parameters of mixed effect models (with site identity adopted as random factor) testing for effects of *P. cerasifera* percentage cover on plant species diversity metrics and community weighted means (CWMs) of plants' functional traits and ecological indicator values (EIV)

Variable	Estimate	SE	<i>t/z</i>	<i>P</i>	RE SD	R_m^2	R_c^2
<i>Taxonomical diversity</i>							
Species richness:							
(Intercept)	3.263	0.044	73.120	< 0.001	< 0.001	0.299	0.299
<i>P. cerasifera</i> cover	0.004	< 0.001	< 0.001	< 0.001			
Shannon's index:							
(Intercept)	1.968	0.074	26.459	< 0.001	0.051	0.230	0.251
<i>P. cerasifera</i> cover	0.005	0.001	3.364	< 0.001			
<i>Functional diversity</i>							
Functional richness SES:							
(Intercept)	0.835	0.191	4.365	< 0.001	0.129	0.010	0.037
<i>P. cerasifera</i> cover	−0.002	0.004	−0.636	0.525			
Functional dispersion SES:							
(Intercept)	−0.259	0.174	−1.484	0.137	0.063	0.201	0.207
<i>P. cerasifera</i> cover	0.012	0.004	3.050	0.002			
Functional divergence SES:							
(Intercept)	0.127	0.235	0.544	0.587	0.301	0.048	0.174
<i>P. cerasifera</i> cover	−0.006	0.004	−1.497	0.134			
Functional evenness SES:							
(Intercept)	−0.121	0.252	−0.484	0.629	0.286		
<i>P. cerasifera</i> cover	< 0.001	0.005	0.174	0.862			
<i>Phylogenetic diversity</i>							
Faith's index:							
(Intercept)	−1.863	0.089	−20.817	< 0.001	< 0.001	0.071	0.071
<i>P. cerasifera</i> cover	0.003	0.002	1.663	0.096			
<i>CWMs of plants' functional traits</i>							
CWM of canopy height:							
(Intercept)	1.267	0.039	31.790	< 0.001	0.041	0.003	0.079
<i>P. cerasifera</i> cover	< −0.001	< 0.001	−0.370	0.708			
CWM of seed mass:							
(Intercept)	1.565	0.122	12.766	< 0.001	0.142	0.003	0.103
<i>P. cerasifera</i> cover	< −0.001	0.002	−0.404	0.686			
CWM of leaf dry matter content:							
(Intercept)	279.545	5.312	52.620	< 0.001	6.871	0.131	0.249
<i>P. cerasifera</i> cover	−0.251	0.097	−2.580	0.009			
CWM of specific leaf area:							
(Intercept)	293.657	7.949	36.940	< 0.001	14.290	0.027	0.495
<i>P. cerasifera</i> cover	−0.121	0.084	−1.440	0.149			
<i>CWMs of ecological indicator values</i>							
CWM of light EIV:							
(Intercept)	7.111	0.142	49.840	< 0.001	0.247	0.135	0.484
<i>P. cerasifera</i> cover	−0.005	0.001	−3.170	0.001			
CWM of temperature EIV:							
(Intercept)	5.488	0.033	165.070	< 0.001	< 0.001	0.100	0.100
<i>P. cerasifera</i> cover	−0.001	< 0.001	−2.080	0.037			
CWM of soil moisture EIV:							
(Intercept)	5.388	0.094	57.000	< 0.001	0.131	0.093	0.248
<i>P. cerasifera</i> cover	0.003	0.001	2.180	0.029			

Table 3 (continued)

Variable	Estimate	SE	<i>t/z</i>	<i>P</i>	RE SD	R_m^2	R_c^2
CWM of soil fertility EIV:							
(Intercept)	5.899	0.144	40.830	<0.001	0.157	0.086	0.163
<i>P. cerasifera</i> cover	0.005	0.002	1.980	0.047			
CWM of soil reaction EIV:							
(Intercept)	6.277	0.045	138.220	<0.001	<0.001	0.191	0.191
<i>P. cerasifera</i> cover	0.003	0.001	3.040	0.002			

SE standard error, *t/z* test statistic, *P* p-value, *RE SD* standard deviation of random effect, R_m^2 marginal coefficient of determination, R_c^2 conditional coefficient of determination. Statistically significant results are in bold

P. cerasifera cover accounted for about 9% of the variance in both cases, while the study site identity explained about 16% and 7% of the variability, respectively. Considering the CWM of soil reaction EIV, *P. cerasifera* cover contributed to 19% of the variance, with no influence of random effect in shaping this relationship (Table 3).

Discussion

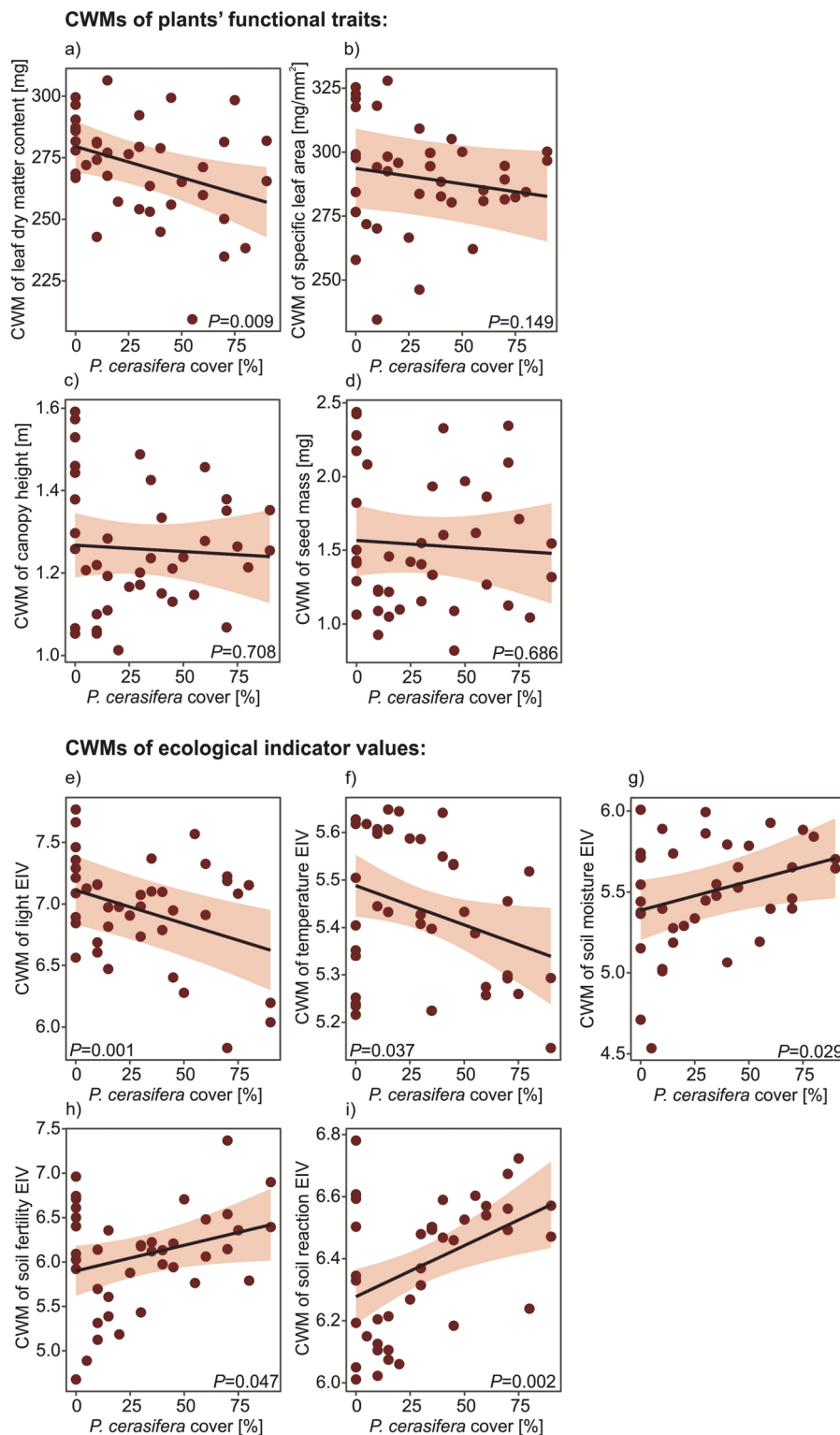
Invasion-driven impact on taxonomical composition

Our results revealed that *P. cerasifera* invasion can substantially shape the species composition of the understory during the early stages of oak-hornbeam forest succession. The CCA analysis showed that plots with lower *P. cerasifera* cover were more similar to each other in terms of understory species composition than plots with higher cover of this non-native tree. Moreover, despite the more predictable and homogeneous species composition in plots with lower intensities of *P. cerasifera* invasion, their community structure was shaped by a larger species pool than heavily invaded plots. Therefore, an increasing cover of *P. cerasifera* can be expected to negatively affect the species composition of the studied forest understory. Similar patterns have been documented for other invasive members of the Rosaceae family, including both taxa closely related to *P. cerasifera*, such as *P. serotina* (e.g. Godefroid et al. 2005; Halarewicz and Żołnierz 2014; Gentili et al. 2019), and more distantly related species, such as *Sorbaronia fallax* nothosubsp. *mitschurinii* (Jagodźiński et al. 2024) or *Spiraea tomentosa* (Wiatrowska et al. 2023).

However, the patterns observed for species composition did not correspond to those identified for the impact of *P. cerasifera* on the taxonomic diversity of the understory. Alongside increasing the cover of *P. cerasifera*, both species richness and Shannon's diversity index increased. This contrasts with the results of previous studies that demonstrate negative impacts of phylogenetically-close invasive Rosaceae representatives on taxonomic diversity (e.g. *P. serotina* Godefroid et al. 2005; Halarewicz and Żołnierz 2014; Gentili et al. 2019), as well as other, less-studied species from the same family (Wiatrowska et al. 2023; Jagodźiński et al. 2024). Nevertheless, other previous studies revealed positive impacts of invasive trees on the understory species richness. For example, Bury and Dyderski (*under review*) also identified positive effects of *P. serotina* invasion on understory taxonomic and functional diversity, however, not in oak-hornbeam forest but in nutrient-poor Scots pine forest.

The positive effect of *P. cerasifera* on taxonomic diversity, on the one hand, may be a consequence of the long-lasting presence of numerous early-successional species typical of open habitats, and associated with historical land use (e.g., ruderal tall herbs, taxa typical of mesic meadows or other non-forest ecosystems) in plots with higher invasion intensities, as revealed by the CCA and threshold indicator taxa analysis. The persistence of these species under high cover of *P. cerasifera* can be explained by the potentially high pressure exerted by large herbivores (e.g., reed deer, European bison, or wild boar) that can use these trees and their surroundings as a food source and resting places. By grazing and browsing, as well as through fine-scale disturbances caused by trampling and rooting, they could significantly contribute

Fig. 5 Visualisation of mixed effect models testing for effects of *P. cerasifera* percentage cover on community weighted means (CWMs) of plants' functional traits (**a–d**) and Ellenberg's ecological indicator values (**e–i**)



to the maintenance of the early-successional character of the understory. That way they can limit the spread of plant species typical of more advanced successional stages (Modrý et al. 2004; Kuijper et al. 2009; Czortek et al. 2024). On the other hand, this positive effect of invasion may be explained by the colonization of plots dominated by *P. cerasifera* by competitors, such as nitrophilous tall herbs.

Effect of *P. cerasifera* invasion on phylogenetic diversity

The patterns observed for taxonomic diversity correspond with the positive impact of *P. cerasifera* invasion on phylogenetic diversity, which contrasts with the findings of the few previous studies on this topic. For instance, Piwczyński et al. (2016) found that *R. pseudoacacia* invasion negatively affected phylogenetic diversity, while Dyderski and Jagodziński (2021) revealed that this effect was forest type-specific. They found higher phylogenetic diversity of understory in *R. pseudoacacia* tree stands than in oak-hornbeam forests, while Scots pine forests on nutrient-rich sites invaded by *P. serotina* supported higher phylogenetic diversity than non-invaded stands. Bury and Dyderski (*under review*) observed that understory phylogenetic diversity decreased considerably with increasing *R. pseudoacacia* biomass in Scots pine forests, but increased in oak-hornbeam forests. However, they did not find any trends for *P. serotina*. In contrast, Livingstone et al. (2020) demonstrated a negative effect of the invasive *Vincetoxicum rossicum* on the species phylogenetic relatedness structure along its invasion gradient, expressed by the increasing abundance of this non-native species.

In our case, the positive effect of *P. cerasifera* on the phylogenetic diversity of the understory can be explained by the presence of more phylogenetically heterogeneous taxa, which could enrich the phylogenetic diversity of plots with high *P. cerasifera* cover, where the role of phylogenetic clustering in shaping the community structure was low. On the other hand, the high phylogenetic clustering observed in plots with lower *P. cerasifera* cover can be explained by the prevalence of closely-related representatives of Poaceae and Asteraceae, occurring there with high taxonomical richness and abundance. In plots with higher *P. cerasifera* cover, the species' relatedness structure was more random: in addition to the

representatives of the aforementioned families, we identified the pronounced influence of other clades (e.g., Apiaceae, Rosaceae, or Fabaceae), as well as members of families less common in the flora of Central Europe (e.g., Campanulaceae or Urticaceae). Thus, one would expect the supplementation of the community structure by new clades, but not yet their substitution, at the studied successional stages of oak-hornbeam forests. Nevertheless, this positive effect of *P. cerasifera* on phylogenetic diversity was not as strong as revealed for taxonomic diversity. This could be interpreted as a legacy effect of closely related Asteraceae and Poaceae species, still present in relatively large numbers in *P. cerasifera*-dominated plots, but occurring in lower abundance compared to plots with lower invasion intensity.

P. cerasifera invasion shapes the community assembly rules

For two of the five analysed functional diversity parameters, we found a strong positive effect of *P. cerasifera* invasion on shaping the functional composition of the understory (i.e. functional dispersion SES). However, to date, only a few studies have assessed the effects of invasive trees on the functional diversity of forest' understory. For instance, Sitzia et al. (2018) and Terwei et al. (2016) found positive effects of invasive trees on functional composition. Chabrierie et al. (2010) found that Rao quadratic entropy was one-third lower in stands invaded by *P. serotina* compared to non-invaded stands. Dyderski and Jagodziński (2021), in turn, observed species-specific effects of invasive trees on the functional diversity of temperate forest understories. They found no influence of the studied non-native tree species on functional dispersion. Regarding functional richness, they reported no effects of *R. pseudoacacia*, negative effects of *Quercus rubra*, and no impact of *P. serotina* invasion, except for a positive effect in artificial Scots pine forests. Bury and Dyderski (*under review*) found an increase in functional dispersion of the understory along the abundance gradient of *R. pseudoacacia* in Scots pine tree stands, while a decrease was observed in oak-hornbeam forests. However, they found no impact on functional richness. Fernandez et al. (2021) observed a decrease in functional richness and functional dispersion along the density gradient of the invasive *Ligustrum lucidum*, while Livingstone

et al. (2020) reported similar trends along the cover gradient of *Vincetoxicum rossicum*. Similarly, invasive trees in Brazilian Atlantic forests were found to decrease functional richness (Larsen et al. 2024). Henry et al. (2021), in turn, observed a quadratic relationship between increasing the cover of *Tamarix* spp. and functional dispersion of the herb layer in riparian plant communities.

It is tempting to assume that the positive effects of *P. cerasifera* on functional dispersion SES could be interpreted in terms of increasing the role of niche differentiation in shaping community assembly processes in the invasion gradient. This may suggest that the dissimilarities in the plant species' realized niches would be higher in plots dominated by *P. cerasifera*. This was demonstrated, for instance, by Hejda et al. (2017), who found that the invasive *R. pseudoacacia* can create new niches for more nitrophilous and hemerobic plant species. Nevertheless, when inspecting the CWMs of EIVs in our case, *P. cerasifera* invasion led to a decrease in the contribution of light-demanding and thermophilous species, in favour of species preferring higher soil moisture, higher soil pH, and nitrophilous taxa in plots with higher invasion intensities. This may explain why the degree of filled niche space (indicated by functional richness SES) and the regularity of the species' realized niche distribution within an assemblage (indicated by functional evenness SES) remained constant along the *P. cerasifera* invasion gradient. One possible explanation of this pattern may be the replacement of plant functional types typical of open habitats by those with higher competitive abilities, suggesting an invasion-driven functional turnover of the species' realized niches. The CCA and threshold indicator taxa analysis results may support this interpretation, revealing, for instance, that the optimal occurrence of *A. elatius*, a diagnostic species for *Arrhenatherion elatioris* meadows (code 6510 in the NATURA 2000 network), was found in plots with lower *P. cerasifera* invasion intensities. In contrast, perennial nitrophilous tall herbs with a predominantly competitive strategy showed their optimum (e.g., *U. dioica* or *G. urbanum*), and higher affinities (e.g., *A. podagraria*, *A. sylvestris*, *G. aparine*, *L. communis* or *R. idaeus*) to plots with higher *P. cerasifera* cover.

The colonization of plots by species with higher EIV-N and EIV-R values could be triggered by the potential effect of *P. cerasifera* on the decomposition

rate of the leaf litter (Kislo et al. 2024), a phenomenon that requires further detailed examination. Nevertheless, we might expect that *P. cerasifera* may decompose at a rate similar to that of the phylogenetically closely related *P. serotina* (Horodecki et al. 2019). This may potentially accelerate the overall rate of plant biomass decomposition in areas invaded by *P. cerasifera*, leading to an increased release of nutrients into the soil, as reported for other invasive plant species (Halabuk and Gerhátoová 2011; Zukswert and Prescott 2017; Gaggini et al. 2018). This may indicate the potential role of *P. cerasifera* as an ecosystem engineer, which, through its hypothesized impact on decomposition, would promote species of higher nitrogen and lower soil acidity demands. This would be in line with the expected impacts of *P. serotina* and *R. pseudoacacia* in Scots pine forests (Halarewicz and Żołniercz 2014; Bury and Dyderski *under review*). The relationships presented above may thus indicate a considerable influence of *P. cerasifera* invasion on increasing the importance of interspecific competition while reducing the role of habitat filtering in shaping the community assembly processes.

Another confirmation of the increasing role of interspecific competition in shaping the functional composition of understory along the invasion gradient may be a negative relationship between the increasing cover of *P. cerasifera* and leaf dry matter content CWM. Therefore, one may expect that with increasing *P. cerasifera* invasion intensity, the proportion of species indicative of the prevalence of habitat filtering and environmental stress in shaping the community assembly rules could decrease. Apart from graminoids typical of mesic meadows, this group of species could include pioneer species (i.e. ruderal tall herbs), whose leaf dry matter content tends to be generally lower than that of species indicative of more advanced successional stages and therefore more acquisitive life strategies (Pérez-Harguindeguy et al. 2013). This pattern corresponds with a slightly negative effect of *P. cerasifera* invasion on functional divergence SES. This relationship suggests that species with extreme functional trait values, which differ substantially from the functional trait combinations of the dominating species or subordinates (Ulrich et al., *under review*), began to reduce their abundance as the cover of *P. cerasifera* increased, coinciding with the increasing dominance of species with more similar functional traits.

Conclusions

Our study provided the first assessment of *P. cerasifera* impact on the understory diversity across its invasion gradient, as well as provided another evidence of the effects of invasive trees on the forest ecosystem functioning. The demonstrated positive impacts of *P. cerasifera* invasion on taxonomical, phylogenetic, and functional composition may exert long-term consequences on the understory structure of early successional stages of oak-hornbeam forests. The supplementation by perennial nitrophilous tall herbs phylogenetically and functionally distinct from non-forest species, may reduce the relative importance of habitat filtering in shaping community assembly processes. In this context, *P. cerasifera* may inhibit the colonisation of the understory by typical forest species, early signs of which would be observed in vegetation patches where *P. cerasifera* dominated the tree layer. In the context of the potential engineering abilities of *P. cerasifera*, increased competition under its higher cover may lower the survival and recruitment of native post-pioneer tree seedlings, thereby altering the mechanisms of the oak-hornbeam forest succession, which would differ substantially from successional trajectories observed for non-invaded forest patches. Our conclusions are crucial for understanding the impact of *P. cerasifera* invasion in the secondary forest succession and developing management actions to understand the long-term effects of its spread.

Author contributions PC: Conceptualization, Investigation, Data curation, Formal analysis, Methodology, Resources, Visualization, Writing—original draft, Writing—review & editing; WA: Investigation, Writing—original draft, Writing—review & editing; MKD: Conceptualization, Formal analysis, Visualization, Writing—original draft, Writing—review & editing.

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Data availability Raw data with all R scripts used to conduct statistical analyses are presented in Online Resource 2.

Declarations

Conflict of interest The authors have no relevant financial or non-financial interests to disclose.

Ethical approval The study did not involve human or animal participants as study subjects.

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References

- Adamowski W, Bomanowska A (2011) Forest return on an abandoned field - secondary succession under monitored conditions. *Acta Univ Lodz Folia Biol Oecol* 7:49–73
- Adamowski W, Dvorak L, Ramanjuk I (2002) Atlas of alien woody species of the Białowieża primeval forest. *Phytocoenosis Supplementum Cartographiae Geobotanicae* 14:1–301
- Adamowski W, Wołkowycki D (2014) Flora roślin naczyniowych. In: Wołkowycki D (ed) *Przyroda okolic wsi Haćki na Równinie Bielskie*. Fundacja “Zielone Płuca Polski,” Białystok, pp 71–98
- Aerts R, Ewald M, Nicolas M, Piat J, Skowronek S, Lenoir J, Hattab T, Garzón-López CX, Feilhauer H, Schmidtlein S, Rocchini D, Decocq G, Somers B, Van De Kerchove R, Denef K, Honnay O (2017) Invasion by the alien tree *Prunus serotina* alters ecosystem functions in a temperate deciduous forest. *Front Plant Sci* 8:179. <https://doi.org/10.3389/fpls.2017.00179>
- Anibaba QA, Dyderski MK, Woźniak G, Jagodziński AM (2025) The inhibitory tendency of *Calamagrostis epigejos* and *Solidago* spp. depends on the successional stage in postindustrial vegetation. *Land Degrad Dev* 36:121–132. <https://doi.org/10.1002/ldr.5348>
- Baker ME, King RS, Kahle D (2023) TITAN2: Threshold Indicator Taxa Analysis <https://doi.org/10.32614/CRAN.package.TITAN2>. (Accessed 29 Apr 2025)
- Barney JN, Tekiel DR, Barrios-Garcia MN, Dimarco RD, Hufbauer RA, Leipzig-Scott P, Nuñez MA, Pauchard A, Pyšek P, Vítková M, Maxwell BD (2015) Global invader impact network (GIIN): toward standardized evaluation of the ecological impacts of invasive plants. *Ecol Evol* 5:2878–2889. <https://doi.org/10.1002/ece3.1551>
- Blackburn TM, Pyšek P, Bacher S, Carlton JT, Duncan RP, Jarošík V, Wilson JR, Richardson DM (2011) A proposed unified framework for biological invasions. *Trends Ecol Evol* 26:333–339. <https://doi.org/10.1016/j.tree.2011.03.023>

- Brooks ME, Kristensen K, Benthem KJ, van Magnusson A, Berg CW, Nielsen A, Skaug HJ, Mächler M, Bolker BM (2017) glmm TMB balances speed and flexibility among packages for Zero-inflated generalized linear mixed modeling. *R J* 9:378. <https://doi.org/10.32614/RJ-2017-066>
- Brundu G, Pauchard A, Pyšek P, Pergl J, Bindewald AM, Brunori A, Canavan S, Campagnaro T, Celesti-Grapow L, Dechoum MdeS, Dufour-Dror J-M, Essl F, Flory SL, Genovesi P, Guarino F, Guangzhe L, Hulme PE, Jäger H, Kettle CJ, Krumm F, Langdon B, Lapin K, Lozano V, Roux JLL, Novoa A, Nuñez MA, Porté AJ, Silva JS, Schaffner U, Sitzia T, Tanner R, Tshidada N, Vítková M, Westergren M, Wilson JR, Richardson DM (2020) Global guidelines for the sustainable use of non-native trees to prevent tree invasions and mitigate their negative impacts. *NeoBiota* 61:65–116. <https://doi.org/10.3897/neobiota.61.58380>
- Bury S, Jagodziński AM, Dyderski MK (2024) In search of per capita effects of *Prunus serotina* Ehrh. invasion on temperate forest understory alpha diversity. *Biologia* 79:3011–3025. <https://doi.org/10.1007/s11756-024-01766-7>
- Cadotte MW, Carscadden K, Mirotchnick N (2011) Beyond species: functional diversity and the maintenance of ecological processes and services. *J Appl Ecol* 48:1079–1087. <https://doi.org/10.1111/j.1365-2664.2011.02048.x>
- Carboneras C, Genovesi P, Vilà M et al (2018) A prioritised list of invasive alien species to assist the effective implementation of EU legislation. *J Appl Ecol* 22:539–547. <https://doi.org/10.1111/1365-2664.12997>
- Carroll IT, Cardinale BJ, Nisbet RM (2011) Niche and fitness differences relate the maintenance of diversity to ecosystem function. *Ecology* 92:1157–1165. <https://doi.org/10.1890/10-0302.1>
- Castro-Díez P, Godoy O, Alonso A, Gallardo A, Saldaña A (2014) What explains variation in the impacts of exotic plant invasions on the nitrogen cycle? A meta-analysis. *Ecol Lett* 17:1–12. <https://doi.org/10.1111/ele.12197>
- Chabrierie O, Loinard J, Perrin S, Saguez R, Decocq G (2010) Impact of *Prunus serotina* invasion on understory functional diversity in a European temperate forest. *Biol Invasions* 12:1891–1907. <https://doi.org/10.1007/s10530-009-9599-9>
- Chesson P (2000) Mechanisms of maintenance of species diversity. *Annu Rev Ecol Syst* 31:343–366. <https://doi.org/10.1146/annurev.ecolsys.31.1.343>
- Chytrý M, Tichý L, Dřevojan P, Sádlo J, Zelený D (2018) Ellenberg-type indicator values for the Czech flora. *Preslia* 90:83–103. <https://doi.org/10.23855/preslia.2018.083>
- Chytrý M, Danihelka J, Kaplan Z et al (2021) Pladias database of the Czech flora and vegetation. *Preslia* 93:1–87. <https://doi.org/10.23855/preslia.2021.001>
- Corenblit D, Steiger J, Tabacchi E, González E, Planty-Tabacchi A-M (2014) Ecosystem engineers modulate exotic invasions in riparian plant communities by modifying hydrogeomorphic connectivity. *River Res Appl* 30:45–59. <https://doi.org/10.1002/rra.2618>
- Czortek P (2023) Landscape-driven effects on taxonomic, functional, and phylogenetic diversity of vegetation development on sand-gravel pits of early successional stages. *Ecol Informatics* 76:102123. <https://doi.org/10.1016/j.ecoinf.2023.102123>
- Czortek P, Eycott AE, Grytnes J-A, Delimat A, Kapfer J, Jarszewicz B (2018) Effects of grazing abandonment and climate change on mountain summits flora: a case study in the Tatra Mts. *Plant Ecol* 219:261–276. <https://doi.org/10.1007/s11258-018-0794-6>
- Czortek P, Orczewska A, Dyderski MK (2021) Niche differentiation, competition or habitat filtering? Mechanisms explaining co-occurrence of plant species on wet meadows of high conservation value. *J Veg Sci* 32:e12983. <https://doi.org/10.1111/jvs.12983>
- Czortek P, Królak E, Borkowska L, Bielecka A (2023) Effects of surrounding landscape on the performance of *Solidago canadensis* L. and plant functional diversity on heavily invaded post-agricultural wastelands. *Biol Invasions*. <https://doi.org/10.1007/s10530-023-03050-2>
- Czortek P, Adamowski W, Kamionka-Kancłerska K, Karpińska O, Zalewski A, Dyderski MK (2024) Patterns of *Prunus cerasifera* early invasion stages into a temperate primeval forest. *Biol Invasions* 26:633–647. <https://doi.org/10.1007/s10530-023-03188-z>
- Díaz S, Kattge J, Cornelissen JHC et al (2016) The global spectrum of plant form and function. *Nature* 529:167–171. <https://doi.org/10.1038/nature16489>
- Diniz-Filho JAF, de Sant'Ana CER, Bini LM (1998) An eigenvector method for estimating phylogenetic inertia. *Evolution* 52:1247–1262. <https://doi.org/10.1111/j.1558-5646.1998.tb02006.x>
- Dobrzycka-Kraheil A, Medina-Villar S (2020) Alien species of mediterranean origin in the Baltic sea region: current state and risk assessment. *Environ Rev* 28:339–356. <https://doi.org/10.1139/er-2019-0074>
- Dyderski MK, Jagodziński AM (2021) Impacts of invasive trees on alpha and beta diversity of temperate forest understories. *Biol Invasions* 23:235–252. <https://doi.org/10.1007/s10530-020-02367-6>
- Dzwonko Z (2001) Assessment of light and soil conditions in ancient and recent woodlands by Ellenberg indicator values. *J Appl Ecol* 38:942–951. <https://doi.org/10.1046/j.1365-2664.2001.00649.x>
- Ellenberg H, Leuschner C (2010) Vegetation Mitteleuropas mit den Alpen in ökologischer, dynamischer und historischer Sicht. UTB, Stuttgart
- Ellison AM, Bank MS, Clinton BD, Colburn EA, Elliott K, Ford CR, Foster DR, Kloeppel BD, Knoepp JD, Lovett GM, Mohan J, Orwig DA, Rodenhouse NL, Sobczak WV, Stinson KA, Stone JK, Swan CM, Thompson J, Von Holle B, Webster JR (2005) Loss of foundation species: consequences for the structure and dynamics of forested ecosystems. *Front Ecol Environ* 3:479–486. [https://doi.org/10.1890/1540-9295\(2005\)003\[0479:LOFSCF\]2.0.CO;2](https://doi.org/10.1890/1540-9295(2005)003[0479:LOFSCF]2.0.CO;2)
- Engel M, Nyssen B, Desie E, den Ouden J, Raats L, Hagemann U (2024) Managing black cherry (*Prunus serotina* Ehrh.) in European forests: insights from native and non-native ranges. *For Ecol Manage* 562:121959. <https://doi.org/10.1016/j.foreco.2024.121959>
- Evangelista A, Frate L, Carranza ML, Attorre F, Pelino G, Stanisci A (2016) Changes in composition, ecology and structure of high-mountain vegetation: a re-visitation

- study over 42 years. *AoB Plants* 8:plw004. <https://doi.org/10.1093/aobpla/plw004>
- Fernandez RD, Castro-Díez P, Aragón R, Pérez-Harguindeguy N (2021) Changes in community functional structure and ecosystem properties along an invasion gradient of *Ligustrum lucidum*. *J Veg Sci* 32:e13098. <https://doi.org/10.1111/jvs.13098>
- Fox J, Weisberg S, Price B, Adler D, Bates D, Baud-Bovy G, Bolker B, Ellison S, Firth D, Friendly M, Gorjanc G, Graves S, Heiberger R, Krivitsky P, Laboissiere R, Maechler M, Monette G, Murdoch D, Nilsson H, Ogle D, Ripley B, Short T, Venables W, Walker S, Winsemius D, Zeileis A, R-Core (2024) car: Companion to Applied Regression. <https://doi.org/10.32614/CRAN.package.car> (Accessed 29 Apr 2025)
- Gaggini L, Rusterholz H-P, Baur B (2018) The invasive plant *Impatiens glandulifera* affects soil fungal diversity and the bacterial community in forests. *Appl Soil Ecol* 124:335–343. <https://doi.org/10.1016/j.apsoil.2017.11.021>
- Gentili R, Ferrè C, Cardarelli E, Montagnani C, Bogliani G, Citterio S, Comolli R (2019) Comparing negative impacts of *Prunus serotina*, *Quercus rubra* and *Robinia pseudoacacia* on native forest ecosystems. *Forests* 10:842. <https://doi.org/10.3390/f10100842>
- Gilliam FS, Roberts MR (2003) Interaction Between the Herbaceous Layer and Overstory Canopy of Eastern Forests. A Mechanism for Linkage. In: Gilliam FS, Roberts MR (eds) *The herbaceous layer in forests of eastern North America*. Oxford University Press, New York, pp 198–223
- Godefroid S, Phartyal SS, Weyembergh G, Koedam N (2005) Ecological factors controlling the abundance of non-native invasive black cherry (*Prunus serotina*) in deciduous forest understory in Belgium. *For Ecol Manage* 210:91–105. <https://doi.org/10.1016/j.foreco.2005.02.024>
- Götzenberger L, De Bello F, Bräthen KA, Davison J, Dubuis A, Guisan A, Lepš J, Lindborg R, Moora M, Pärtel M, Pellissier L, Pottier J, Vittoz P, Zobel K, Zobel M (2012) Ecological assembly rules in plant communities—approaches, patterns and prospects. *Biol Rev* 87:111–127. <https://doi.org/10.1111/j.1469-185X.2011.00187.x>
- Grime JP (2006) *Plant strategies, vegetation processes, and ecosystem properties*. John Wiley & Sons, Hoboken
- Halabuk A, Gerhátová K (2011) Comparative study of leaf litter decomposition of exotic and native species in an ecotop of the hornbeam-oak forest near Báb village, SW Slovakia. *Folia Oecol* 38:17–27
- Halarewicz A, Żołniercz L (2014) Changes in the understory of mixed coniferous forest plant communities dominated by the American black cherry (*Prunus serotina* Ehrh.). *For Ecol Manage* 313:91–97. <https://doi.org/10.1016/j.foreco.2013.11.006>
- Hartig F (2025) DHARMA: Residual Diagnostics for Hierarchical (Multi-Level / Mixed) Regression Models. R package version 0.4.7. <https://doi.org/10.32614/CRAN.package.DHARMA> (Accessed 29 Apr 2025)
- Hejda M, Hanzelka J, Kadlec T, Štrobl M, Pyšek P, Reif J (2017) Impacts of an invasive tree across trophic levels: species richness, community composition and resident species' traits. *Divers Distrib* 23:997–1007. <https://doi.org/10.1111/ddi.12596>
- Henry AL, González E, Bourgeois B, Sher AA (2021) Invasive tree cover covaries with environmental factors to explain the functional composition of riparian plant communities. *Oecologia* 196:1139–1152. <https://doi.org/10.1007/s00442-021-04990-z>
- HilleRisLambers J, Adler PB, Harpole WS, Levine JM, Mayfield MM (2012) Rethinking community assembly through the lens of coexistence theory. *Annu Rev Ecol Evol Syst* 43:227–248. <https://doi.org/10.1146/annurev-ecolsys-110411-160411>
- Horodecki P, Nowiński M, Jagodziński AM (2019) Advantage of mixed tree stands in restoration of upper soil layers on post-mining sites: a five-year leaf litter decomposition experiment. *Land Degrad Dev* 30:3–13. <https://doi.org/10.1002/ldr.3194>
- Jagodziński AM, Horodecki P, Jasińska AK, Maliński T, Pilarek Z, Woźniak K, Wrońska-Pilarek D, Zieliński J, Dyderski MK (2024) Invasive *Sorbaronia fallax* nothosubsp. *mitschurinii* affects temperate Scots pine forest biodiversity and functioning. *For Ecol Manage* 568:122147. <https://doi.org/10.1016/j.foreco.2024.122147>
- Jin Y, Qian H (2022) V.phylomaker2: an updated and enlarged R package that can generate very large phylogenies for vascular plants. *Plant Divers* 44:335–339. <https://doi.org/10.1016/j.pld.2022.05.005>
- Kislo K, Mazurkiewicz MT, Kuberski Ł, Dyderski M, Rawlik K, Czortek P (2024). *Prunus cerasifera* decomposes faster than surrounding graminoids. In: Białowieża Ecology Conference – Temperate Forests in the Anthropocene. Disturbances, species, humans and ecosystem functioning. 15–20 September 2024, Białowieża, pp 15–20.
- Kleyer M, Bekker RM, Knevel IC, Bakker JP, Thompson K, Sonnenschein M, Poschlod P, Van Groenendael JM, Klimeš L, Klimešová J, Klotz S, Rusch GM, Hermy M, Adriaens D, Boedeltje G, Bossuyt B, Dannemann A, Endels P, Götzenberger L, Hodgson JG, Jackel A-K, Kühn I, Kunzmann D, Ozinga WA, Römermann C, Stadler M, Schlegelmilch M, Steendam HJ, Teckenberg O, Wilmann B, Cornelissen JH, Eriksson O, Garnier E, Peco B (2008) The LEDA Traitbase: a database of life-history traits of the Northwest European flora. *J Ecol* 96:1266–1274. <https://doi.org/10.1111/j.1365-2745.2008.01430.x>
- Klotz S, Kühn I, Durka W (2002) BIOLFLOR – Eine Datenbank zu biologisch-ökologischen Merkmalen der Gefäßpflanzen in Deutschland. Schriftenreihe für Vegetationskunde. Bundesamt für Naturschutz, Bonn
- Kowarik I (1995) Time lags in biological invasions with regard to the success and failure of alien species. In: Pyšek P, Prach K, Rejmánek M, Wade M (eds) *Plant invasions: general aspects and special problems*. SPB Academic Publishing, Amsterdam, pp 15–38
- Kuijper DPJ, Cromsigt JPGM, Churski M, Adam B, Jędrzejewska B, Jędrzejewski W (2009) Do ungulates preferentially feed in forest gaps in European temperate forest? *For Ecol Manage* 258:1528–1535. <https://doi.org/10.1016/j.foreco.2009.07.010>

- Kumschick S, Gaertner M, Vilà M, Essl F, Jeschke JM, Pyšek P, Ricciardi A, Bacher S, Blackburn TM, Dick JTA, Evans T, Hulme PE, Kühn I, Mrugała A, Pergl J, Rabitsch W, Richardson DM, Sendek A, Winter M (2015) Ecological impacts of alien species: quantification, scope, caveats, and recommendations. *Bioscience* 65:55–63. <https://doi.org/10.1093/biosci/biu193>
- Kurek P, Wiatrowska B, Piechnik Ł, Holeksa J (2024) Phenological gap in fruiting period and dispersal of seeds from alien fleshy-fruited plants by medium-sized carnivores in temperate forests of central Europe. *NeoBiota* 93:321–337. <https://doi.org/10.3897/neobiota.93.128008>
- Laliberté E, Legendre P (2010) A distance-based framework for measuring functional diversity from multiple traits. *Ecology* 91:299–305. <https://doi.org/10.1890/08-2244.1>
- Larsen JG, Da Silva AC, De Sá DM, De Freitas EM, Gomes JP, Stedille LIB, Carvalho J, Higuchi P (2024) Diversity, species coexistence and functional composition patterns in subtropical Atlantic Forests invaded by non-native trees. *Funct Ecol* 38:327–337. <https://doi.org/10.1111/1365-2435.14491>
- Lázaro-Lobo A, Fernandez RD, Alonso Á, Cruces P, Cruz-Alonso V, Ervin GN, Gallardo A, Granda E, Gómez-Gras D, Marchante H, Moreno-Fernández D, Saldaña A, Silva JS, Castro-Díez P (2025) Worldwide comparison of carbon stocks and fluxes between native and non-native forests. *Biol Rev*. <https://doi.org/10.1111/brv.13176>
- Livingstone SW, Isaac ME, Cadotte MW (2020) Invasive dominance and resident diversity: unpacking the impact of plant invasion on biodiversity and ecosystem function. *Ecol Monogr* 90:e01425. <https://doi.org/10.1002/ecm.1425>
- Lüdecke D (2018) ggeffects: tidy data frames of marginal effects from regression models. *J Open Source Softw* 3:772. <https://doi.org/10.21105/joss.00772>
- Maitner BS, Boyle B, Casler N, Condit R, Donoghue J, Durán SM, Guaderrama D, Hinchliff CE, Jørgensen PM, Kraft NJB, McGill B, Merow C, Morueta-Holme N, Peet RK, Sandel B, Schildhauer M, Smith SA, Svenning J-C, Thiers B, Violle C, Wiser S, Enquist BJ (2018) The BIEN R package: a tool to access the Botanical Information and Ecology Network (BIEN) database. *Methods Ecol Evol* 9:373–379. <https://doi.org/10.1111/2041-210X.12861>
- Mason NWH, Moullot D, Lee WG, Wilson JB (2005) Functional richness, functional evenness and functional divergence: the primary components of functional diversity. *Oikos* 111:112–118. <https://doi.org/10.1111/j.0030-1299.2005.13886.x>
- Mayfield MM, Levine JM (2010) Opposing effects of competitive exclusion on the phylogenetic structure of communities. *Ecol Lett* 13:1085–1093. <https://doi.org/10.1111/j.1461-0248.2010.01509.x>
- Modrý M, Hubený D, Rejšek K (2004) Differential response of naturally regenerated European shade tolerant tree species to soil type and light availability. *For Ecol Manage* 188:185–195. <https://doi.org/10.1016/j.foreco.2003.07.029>
- Mouchet MA, Villéger S, Mason NWH, Moullot D (2010) Functional diversity measures: an overview of their redundancy and their ability to discriminate community assembly rules. *Funct Ecol* 24:867–876. <https://doi.org/10.1111/j.1365-2435.2010.01695.x>
- Mudrák O, Doležal J, Vítová A, Lepš J (2019) Variation in plant functional traits is best explained by the species identity: stability of trait-based species ranking across meadow management regimes. *Funct Ecol* 33:746–755. <https://doi.org/10.1111/1365-2435.13287>
- Nakagawa S, Cuthill IC (2007) Effect size, confidence interval and statistical significance: a practical guide for biologists. *Biol Rev* 82:591–605. <https://doi.org/10.1111/j.1469-185X.2007.00027.x>
- Nicod C, Gillet F (2021) Recent changes in mountain hay meadows of high conservation value in eastern France. *Appl Veg Sci* 24:e12573. <https://doi.org/10.1111/avsc.12573>
- Novoa A, Richardson DM, Pyšek P, Meyerson LA, Bacher S, Canavan S, Catford JA, Čuda J, Essl F, Foxcroft LC, Genovesi P, Hirsch H, Hui C, Jackson MC, Kueffer C, Le Roux JJ, Measey J, Mohanty NP, Moodley D, Müller-Schärer H, Packer JG, Pergl J, Robinson TB, Saul W-C, Shackleton RT, Visser V, Weyl OLF, Yannelli FA, Wilson JR (2020) Invasion syndromes: a systematic approach for predicting biological invasions and facilitating effective management. *Biol Invasions* 22:1801–1820. <https://doi.org/10.1007/s10530-020-02220-w>
- Nyssen B, Ouden JD, Bindewald A, Brancalion P, Kremer K, Lapin K, Raats L, Schatzdorfer E, Stanturf J, Verheyen K, Muys B (2024) Established invasive tree species offer opportunities for forest resilience to climate change. *Curr Forestry Rep* 10:456–486. <https://doi.org/10.1007/s40725-024-00232-6>
- Oksanen J, Blanchet FG, Kindt R, Legendre P, Michin PR, O'Hara RB, Simpson GL, Solymos P, Henry M, Stevens H, Wagner H (2025) “vegan” 2.3.3. - Community Ecology Package. <https://doi.org/10.32614/CRAN.package.vegan> (Accessed 29 Apr 2025)
- Olden JD, Comte L, Giam X (2018) The homococene: a research prospectus for the study of biotic homogenisation. *NeoBiota* 37:23–36. <https://doi.org/10.3897/neobiota.37.22552>
- Pairon M, Jonard M, Jacquemart A-L (2006) Modeling seed dispersal of black cherry, an invasive forest tree: how microsatellites may help? *Can J for Res* 36:1385–1394. <https://doi.org/10.1139/x06-018>
- Parker IM, Simberloff D, Lonsdale WM, Goodell K, Wonham M, Kareiva PM, Williamson MH, Von Holle B, Moyle PB, Byers JE, Goldwasser L (1999) Impact: toward a framework for understanding the ecological effects of invaders. *Biol Invasions* 1:3–19. <https://doi.org/10.1023/A:1010034312781>
- Penone C, Davidson AD, Shoemaker KT, Di Marco M, Rondinini C, Brooks TM, Young BE, Graham CH, Costa GC (2014) Imputation of missing data in life-history trait datasets: which approach performs the best? *Methods Ecol Evol* 5:961–970. <https://doi.org/10.1111/2041-210X.12232>
- Pérez-Harguindeguy N, Díaz S, Garnier E, Lavorel S, Poorter H, Jaureguiberry P, Bret-Harte MS, Cornwell WK, Craine JM, Gurvich DE, Urcelay C, Veneklaas EJ, Reich PB, Poorter L, Wright IJ, Ray P, Enrico L, Pausas JG, De Vos AC, Buchmann N, Funes G, Quétier F, Hodgson

- JG, Thompson K, Morgan HD, Ter Steege H, Sack L, Blonder B, Poschold P, Vaieretti MV, Conti G, Staver AC, Aquino S, Cornelissen JHC (2013) New handbook for standardised measurement of plant functional traits worldwide. *Aust J Bot* 61:167. <https://doi.org/10.1071/BT12225>
- Piwczynski M, Puchałka R, Ulrich W (2016) Influence of tree plantations on the phylogenetic structure of understorey plant communities. *For Ecol Manage* 376:231–237. <https://doi.org/10.1016/j.foreco.2016.06.011>
- Pla L, Casanoves F, Di Rienzo J (2011) Quantifying functional biodiversity. Springer, Dordrecht
- Popescu i, Caudullo G (2016) *Prunus cerasifera* in Europe: distribution, habitat, usage and threats. In: San-Miguel-Ayanz J, de Rigo D, Caudullo G, Houston Durrant T, Mauri A (eds) *European Atlas of Forest Tree Species*. Publication Office of the European Union, Luxembourg, p 142.
- POWO (2022) Plants of the World Online. <https://powo.science.kew.org/> (Accessed 29 Apr 2025)
- R Core Team (2025) R: A language and environment for statistical computing. <http://www.R-project.org/> (Accessed 29 Apr 2025)
- Rejmánek M, Richardson DM (2013) Trees and shrubs as invasive alien species - 2013 update of the global database. *Divers Distrib* 19:1093–1094. <https://doi.org/10.1111/ddi.12075>
- Ridding LE, Bullock JM, Pescott OL, Hawes P, Walls R, Pereira MG, Thacker SA, Keenan PO, Dragosits U, Pywell RF (2020) Long-term change in calcareous grassland vegetation and drivers over three time periods between 1970 and 2016. *Plant Ecol* 221:377–394. <https://doi.org/10.1007/s11258-020-01016-1>
- Roy HE, Pauchard A, Stoett PJ, Renard Truong T, Meyerson LA, Bacher S, Galil BS, Hulme PE, Ikeda T, Kavileveetil S, McGeoch MA, Nuñez MA, Ordonez A, Rahlao SJ, Schwindt E, Seebens H, Sheppard AW, Vandvik V, Aleksanyan A, Ansong M, August T, Blanchard R, Brugnoli E, Bukombe JK, Bwalya B, Byun C, Camacho-Cervantes M, Cassey P, Castillo ML, Courchamp F, Dehnen-Schmutz K, Zenni RD, Egawa C, Essl F, Fayvush G, Fernandez RD, Fernandez M, Foxcroft LC, Genovesi P, Groom QJ, González AI, Helm A, Herrera I, Hiremath AJ, Howard PL, Hui C, Ikegami M, Keskin E, Koyama A, Ksenofontov S, Lenzner B, Lipinskaya T, Lockwood JL, Mangwa DC, Martinou AF, McDermott SM, Morales CL, Müllerová J, Mungi NA, Munishi LK, Ojaveer H, Pagad SN, Pallewatta NPKTS, Peacock LR, Per E, Pergl J, Preda C, Pyšek P, Rai RK, Ricciardi A, Richardson DM, Riley S, Rono BJ, Ryan-Colton E, Saeedi H, Shrestha BB, Simberloff D, Tawake A, Tricarico E, Vanderhoeven S, Vicente J, Vilà M, Wanzala W, Werenkraut V, Weyl OLF, Wilson JR, Xavier RO, Ziller SR (2024) Curbing the major and growing threats from invasive alien species is urgent and achievable. *Nat Ecol Evol* 8:1216–1223. <https://doi.org/10.1038/s41559-024-02412-w>
- Santos T (2025) PVR: Phylogenetic eigenvectors regression and phylogenetic signal-representation curve. <https://doi.org/10.32614/CRAN.package.PVR>. (Accessed 29 Apr 2025)
- Sapsford SJ, Brandt AJ, Davis KT, Peralta G, Dickie IA, Gibson RD, Green JL, Hulme PE, Nuñez MA, Orwin KH, Pauchard A, Wardle DA, Peltzer DA (2020) Towards a framework for understanding the context-dependence of impacts of non-native tree species. *Funct Ecol* 34:944–955. <https://doi.org/10.1111/1365-2435.13544>
- Schaffers AP, Sýkora KV (2000) Reliability of Ellenberg indicator values for moisture, nitrogen and soil reaction: a comparison with field measurements. *J Veg Sci* 11:225–244. <https://doi.org/10.2307/3236802>
- Seebens H, Blackburn TM, Dyer EE, Genovesi P, Hulme PE, Jeschke JM, Pagad S, Pyšek P, Winter M, Arianoutsou M, Bacher S, Blasius B, Brundu G, Capinha C, Celesti-Grapo L, Dawson W, Dullinger S, Fuentes N, Jäger H, Kartesz J, Kenis M, Kreft H, Kühn I, Lenzner B, Liebhold A, Mosena A, Moser D, Nishino M, Pearman D, Pergl J, Rabitsch W, Rojas-Sandoval J, Roques A, Rorke S, Rossinelli S, Roy HE, Scalera R, Schindler S, Štajerová K, Tokarska-Guzik B, van Kleunen M, Walker K, Weigelt P, Yamanaka T, Essl F (2017) No saturation in the accumulation of alien species worldwide. *Nat Commun* 8:14435. <https://doi.org/10.1038/ncomm14435>
- Sitzia T, Campagnaro T, Kotze DJ, Nardi S, Ertani A (2018) The invasion of abandoned fields by a major alien tree filters understory plant traits in novel forest ecosystems. *Sci Rep* 8(1):8410. <https://doi.org/10.1038/s41598-018-26493-3>
- Smirnov NS (1965) *Ekzoty Belovežskoj Pušči i ejo okresnostej*. Msc
- Spasojevic MJ, Suding KN (2012) Inferring community assembly mechanisms from functional diversity patterns: the importance of multiple assembly processes. *J Ecol* 100:652–661. <https://doi.org/10.1111/j.1365-2745.2011.01945.x>
- Stekhoven DJ, Bühlmann P (2012) Missforest—non-parametric missing value imputation for mixed-type data. *Bioinformatics* 28:112–118. <https://doi.org/10.1093/bioinformatics/btr597>
- Szymura TH, Szymura M, Macioł A (2014) Bioindication with Ellenberg's indicator values: a comparison with measured parameters in Central European oak forests. *Ecol Indic* 46:495–503. <https://doi.org/10.1016/j.ecolind.2014.07.013>
- Terwei A, Zerbe S, Mölder I, Annighöfer P, Kawaletz H, Ammer C (2016) Response of floodplain understorey species to environmental gradients and tree invasion: a functional trait perspective. *Biol Invasions* 18:2951–2973. <https://doi.org/10.1007/s10530-016-1188-0>
- Tsirogiannis C, Sandel B (2016) PhyloMeasures: a package for computing phylogenetic biodiversity measures and their statistical moments. *Ecography* 39:709–714. <https://doi.org/10.1111/ecog.01814>
- Vilà M, Trillo A, Castro-Díez P, Gallardo B, Bacher S (2024) Field studies of the ecological impacts of invasive plants in Europe. *NeoBiota* 90:139–159. <https://doi.org/10.3897/neobiota.90.112368>
- Villéger S, Mason NWH, Mouillot D (2008) New multidimensional functional diversity indices for a multifaceted framework in functional ecology. *Ecology* 89:2290–2301. <https://doi.org/10.1890/07-1206.1>

- Violle C, Choler P, Borghy B, Garnier E, Amiaud B, Debarros G, Diquelou S, Gachet S, Jolivet C, Kattge J, Lavorel S, Lemauiel-Lavenant S, Loranger J, Mikolajczak A, Munoz F, Olivier J, Viovy N (2015) Vegetation ecology meets ecosystem science: Permanent grasslands as a functional biogeography case study. *Sci Total Environ* 534:43–51. <https://doi.org/10.1016/j.scitotenv.2015.03.141>
- von Arx G, Dobberrin M, Rebetez M (2012) Spatio-temporal effects of forest canopy on understory microclimate in a long-term experiment in Switzerland. *Agric Meteorol* 166–167:144–155
- Wasserstein RL, Lazar NA (2016) The ASA’s statement on p-values: context, process, and purpose. *Am Stat* 70:129–133. <https://doi.org/10.1080/00031305.2016.1154108>
- Weber E (2017) *Invasive Plant Species of the World: A Reference Guide to Environmental Weeds*, 2nd edn. CABI, Wallingford Boston, MA
- Westoby M (1998) A leaf-height-seed (LHS) plant ecology strategy scheme. *Plant Soil* 199:213–227. <https://doi.org/10.1023/A:1004327224729>
- Wiatrowska B, Kurek P, Moron D, Celary W, Chrzanowski A, Trzcinski P, Piechnik Ł (2023) Linear scaling – negative effects of invasive *Spiraea tomentosa* (Rosaceae) on wetland plants and pollinator communities. *NeoBiota* 81:63–90. <https://doi.org/10.3897/neobiota.81.95849>
- Wohlgemuth T, Gossner MM, Campagnaro T, Marchante H, van Loo M, Vacchiano G, Castro-Díez P, Dobrowolska D, Gazda A, Keren S, Keszű Z, Koprowski M, Porta NL, Marozas V, Nygaard PH, Podrážský V, Puchałka R, Reisman-Berman O, Straigytė L, Ylioja T, Pötzelsberger E, Silva JS (2022) Impact of non-native tree species in Europe on soil properties and biodiversity: a review. *NeoBiota* 78:45–69. <https://doi.org/10.3897/neobiota.78.87022>
- Wróbel A, Kurek P, Bogdziewicz M, Dobrowolska D, Zwolak R (2021) Avian dispersal of an invasive oak is modulated by acorn traits and the presence of a native oak. *Forest Ecol Manag.* <https://doi.org/10.1016/j.foreco.2021.119866>
- Zukswert JM, Prescott CE (2017) Relationships among leaf functional traits, litter traits, and mass loss during early phases of leaf litter decomposition in 12 woody plant species. *Oecologia* 185:305–316. <https://doi.org/10.1007/s00442-017-3951-z>

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