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Impacts of invasive trees on alpha and beta diversity of temperate forest understories

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Abstract Despite good recognition of distributions and spread mechanisms of the three most invasive trees in Europe (*Prunus serotina*, *Quercus rubra* and *Robinia pseudoacacia*), their impacts on forest biodiversity are unevenly recognized. Most studies cover only taxonomic alpha diversity, and only a single study included functional and phylogenetic diversity. Using a set of 186 study plots in western Poland we assessed the impacts of these invasive tree species on the alpha and beta taxonomic, functional and phylogenetic diversity of understory vascular plants. Alpha diversity was higher in *R. pseudoacacia* forests and lower in *Q. rubra* forests compared to mature native forests. Compared to non-invaded plantations and forests, alpha diversity was higher in *P. sylvestris* plantations invaded by *P. serotina*, but lower in invaded nutrient-poor *P. sylvestris* forests. Alien species richness was higher and beta diversity was lower in forests invaded by *P. serotina* or *R. pseudoacacia* than in non-invaded forests. In contrast, beta diversity was higher in *Q. rubra* forests than in native forests. We proved that invaded forests differed from non-invaded forests in species composition, but not always with decreased alpha and beta diversity. Impacts of particular invasive species also depended on the reference ecosystem properties (here mature native forests, which did not always have the highest biodiversity), which is a source of inconsistency in previous studies, usually referring to single native ecosystem types.

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Introduction

Invasive alien species are considered one of the most important threats to native biodiversity (Richardson 1998; Mack et al. 2000; Vilà et al. 2011). However, impacts of particular invasive species differ with invader quantity (Kumschick et al. 2015; Pearse et al. 2019), the ability for habitat transformation (Corenblit et al. 2014; Aerts et al. 2017; Castro-Díez et al. 2019)

and recipient community susceptibility to invasion (Lonsdale 1999; Davis et al. 2000). Therefore, both ecological success and impacts on native ecosystems by invasive species are highly context-dependent (Kumschick et al. 2015; Dyderski and Jagodziński 2019a; Sapsford et al. 2020).

Despite numerous studies on the impacts of invasive alien species, most of them focused on the taxonomic diversity of invaded ecosystems (Olden et al. 2018). Even in cases of relatively well-recognized invasive species in regions with good data coverage, recognition of various aspects of biodiversity affected by invasive species is uneven. Review of studies on impacts of the three most frequent invasive tree species in European woodlands (Wagner et al. 2017): *Prunus serotina* Ehrh., *Quercus rubra* L. and *Robinia pseudoacacia* L. (Table 1) revealed that among 71 impacts found, only one considered functional diversity (Chabrerie et al. 2010) and one— phylogenetic diversity (Piwczyński et al. 2016). We also found 17 impacts on proportions of specialist and generalist plant species connected with the filtering of particular traits. In general, invaded stands hosted fewer forest specialists (Woziwoda et al. 2014; Staska et al. 2014; Šibíková et al. 2019) and more alien species (Halarewicz and Żołnierz 2014; Montecchiari et al. 2020). However, in specific conditions trends were different: e.g. in Berlin *R. pseudoacacia* forests hosted fewer alien plant species in the understory than native *Betula pendula* Roth. forests (Trentanovi et al. 2013), and in riparian forests *P. serotina* and *R. pseudoacacia* supported the presence of forest specialists, as these invasive trees occurred in less-disturbed sites within the study area (Terwei et al. 2016). Therefore, knowledge about the impacts of the most frequent invasive trees in European woodlands (Wagner et al. 2017) is scarce and requires a unified assessment regarding multiple types of native ecosystems.

We aimed to assess the impacts of three invasive tree species on species composition and taxonomic, phylogenetic and functional alpha and beta diversity of understory vascular plant communities, in relationship to the mature native forest ecosystems. We hypothesized that the invasive tree species studied will differ in impacts on species diversity and its mechanisms. In detail, we assumed that invasive tree species, due to habitat modification and increased availability of nutrients, will not decrease alpha diversity, but will decrease beta diversity of understory vegetation, by promoting generalist species. We also assumed that diversity of forest specialist species will be more affected by invasive trees than other species.

Materials and methods

Species studied

We studied the effects of three invasive trees: *Prunus serotina*, *Quercus rubra* and *Robinia pseudoacacia*, introduced from the eastern part of North America. All

Table 1 Number of studies comparing particular aspects of understory plant diversity between alien- and native-species dominated forests or along invasive species abundance gradients. Details and references-see Table S1

Biodiversity aspects analyzed	*P. serotina*			*Q. rubra*			*R. pseudoacacia*		
	Positive	No impact	Negative	Positive	No impact	Negative	Positive	No impact	Negative
Taxonomic alpha diversity-Shannon index	0	0	2	0	0	2	1	2	3
Taxonomic alpha diversity-species richness	0	3	4	0	0	4	2	5	5
Taxonomic beta diversity	0	0	0	0	0	0	1	2	1
Alien species richness	3	1	0	0	1	0	1	2	5
Specialists-generalists (impact on specialists)	3	0	3	1	0	4	1	0	7
Functional diversity	0	0	1	0	0	0	0	0	0
Phylogenetic alpha diversity	0	0	0	0	0	0	0	0	1

of them were introduced as ornamental species in the 17th century and then used in forestry and for other uses (Starfinger et al. 2003; Cierjacks et al. 2013; Dyderski et al. 2020). Due to the high decomposition rate of leaf litter, *P. serotina* was widely used as a soil improver (Aerts et al. 2017; Horodecki and Jagodziński 2017). *P. serotina* usually forms a dense shrub layer, decreasing light availability (Muys et al. 1992; Halarewicz and Żołnierz 2014; Jagodziński et al. 2019). *Q. rubra* is a tall tree, growing faster than native oaks and producing slowly decomposing leaf litter, while also decreasing light availability (Dobrylovská 2001; Woziwoda et al. 2019; Dyderski et al. 2020). *R. pseudoacacia* is a pioneer, fast-growing tree species, increasing soil fertility due to its ability to fix nitrogen (Rice et al. 2004; Cierjacks et al. 2013).

Study design

We used a set of 189 study plots (200 m^2 rectangles) established in Wielkopolski National Park (WNP; W Poland; 52° 16′ N, 16° 48′ E; 7584 ha) and described in detail in previous studies (e.g. Dyderski and Jagodziński 2018, 2019b). WNP includes various types of temperate forests, with mean annual temperature of 8.4 °C and mean annual precipitation of 521 mm, for the years 1951–2010. Study plots are systematically arranged, with nine plots in each of 21 blocks (Fig. 1), designed to assess natural spread of the invasive tree species studied. In the center of each study block is a plot within a monoculture of the invasive species studied (in the case of *P. serotina*–*P. sylvestris* monocultures with understories dominated by *P. serotina*). Then, four additional plots were set up off of the N, S, E and W sides of the central plot, nearly outside the alien species monoculture, and another set of four plots, located 30 m away from each of the four additional plots. Three study plots (due to systematic design) occurred in non-forest ecosystems and were excluded from analyses (thus final $n = 186$).

We classified study plots into nine forest types (Fig. 2), similarly as in Dyderski and Jagodziński (2020). This division reflects the phytosociological variability of invaded and uninvaded vegetation. *Fagus sylvatica* dominated forest refers to *Deschampsio flexuose-Fagetum* Schröder 1938, an acidophilous beech forest with scarce understory. *Quercus petraea*-dominated forest refers to *Calamagrostio arundinaceae-Quercetum petraeae* (Hartman 1934) Scamoni et Pass. 1959 acidophilous oak forest, with co-dominance of *Pinus sylvestris* in the overstory. *Quercus-Acer-Tilia* forest refers to *Galio sylvatici-Carpinetum* (R. Tx. 1937) Obverd. 1957, a fertile *Q. petraea*, *Acer platanoides*, *A. pseudoplatanus*, and *Tilia cordata* dominated forest. *Q. rubra* dominated forests refers to former *Q. rubra* plantations, replacing natural *Q. petraea* and *Quercus-Acer-Tilia* forest vegetation, while *Robinia pseudoacacia* dominated forest refers to former *R. pseudoacacia* forests replacing *Quercus-Acer-Tilia* forests. We divided *Pinus sylvestris* forests into two groups: poor (occupying mainly mesic sites of *Leucobryo-Pinetum* (Libbert 1933) W. Mat 1962 and *Calamagrostio arundinaceae-Quercetum petraeae*), and plantation (on nutrient-rich soils, which replaced *Galio sylvatici-Carpinetum*). In each of them we distinguished a variant invaded by *P. serotina*, which spontaneously colonized both types of forests.

We classified plots with more than 500 ind. ha^{-1} of *P. serotina* > 1.3 m tall, as invaded. We also distinguished *Q. rubra* or *R. pseudoacacia* forests, with > 25% (mostly > 75%) of basal area, which originated from former plantations.

Data collection

Within each study plot we recorded vascular plant species and cover using a modified (Barkman et al. 1964), 9-degree Braun-Blanquet scale (r-single individuals, + − few individuals < 1% cover, 1 − < 5% cover, 2 m ≤ 5% cover but numerous individuals, 2a–5–15%, 2b–15–25%, 3–35–50%, 4–50–75%, 5 ≥ 75%) in July of each study year (2015–2018). Then we averaged them at the study plot level. As study plots were permanently marked, we assumed no relocation bias (Verheyen et al. 2018). We also reduced bias connected with observer effect (Lepš and Hadincová 1992) by conducting all field observations by the same author (MKD). Taxonomic nomenclature follows GBIF (2019), as suggested by Seebens et al. (2020) to standardize taxonomy. In total, we found 262 species.

In each plot we assessed the number of species in six guilds: archaeophytes (alien species introduced before 1500, 14 species), neophytes (alien species introduced after 1500, 36 species), all alien species
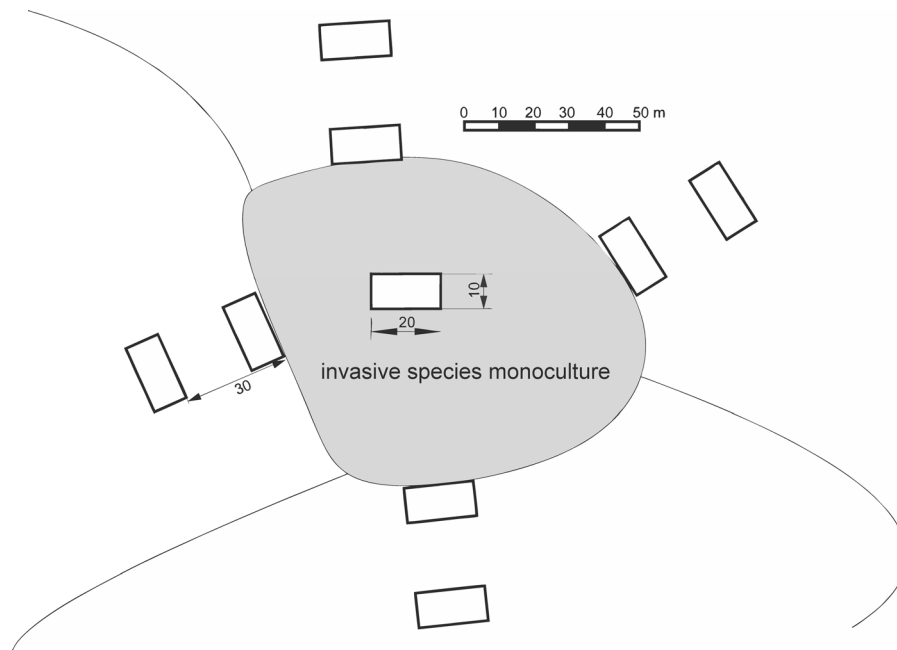
Fig. 1 Schematic arrangement of the study plot blocks (21 blocks, each composed of nine plots). Adapted from Dyderski and Jagodziński (2019c), for the spatial arrangement of forest types within block see supplementary material in Dyderski and Jagodziński (2020)
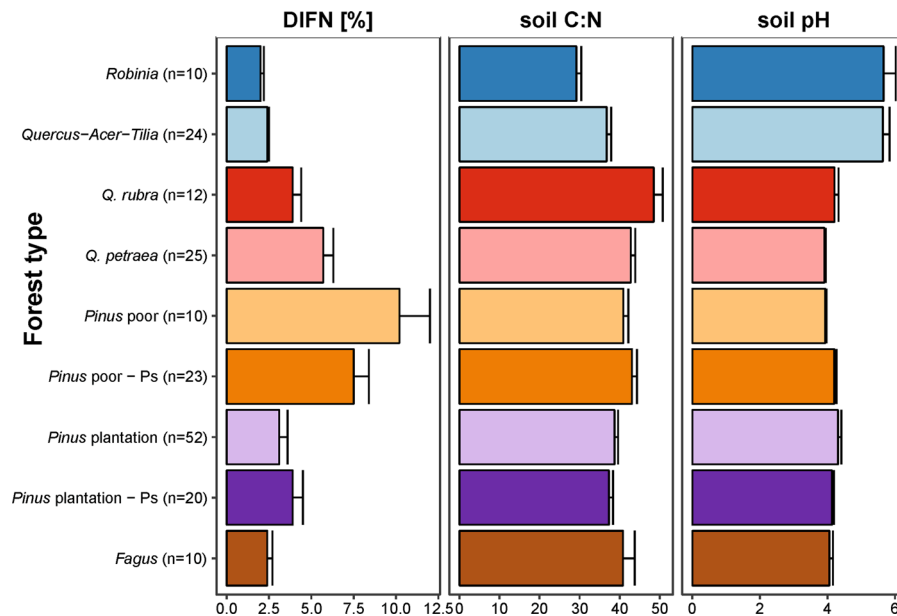

Fig. 2 Mean (+ SE) light availability (DIFN, a fraction of open skylight availability at 0.5 m height), soil C:N ratio and pH (in H$_2$O) by forest type (*Fagus-Fagus sylvatica* dominated forest, *Pinus* plantation-*Pinus sylvestris* forests in fertile sites, *Pinus* plantation-PS-*P. sylvestris* plantation invaded by *Prunus serotina*, *Pinus* poor-*P. sylvestris* forest in poor sites, *Pinus* poor-PS-*P. sylvestris* forest in poor sites invaded by *P. serotina*, *Q. petraea*-acidophilous *Quercus petraea*-dominated forest, *Q. rubra*-*Q. rubra* dominated forests, *Quercus-Acer-Tilia-Q. petraea*, *Acer platanoides*, *A. pseudoplatanus*, *Tilia cordata* dominated fertile forest, *Robinia-Robinia pseudoacacia* dominated forest). For details see Dyderski and Jagodziński (2020)

(sum of archaeophytes and neophytes, 50 species), forest species (see below, 62 species), forest edge and ruderal species (72 species) and ancient forest indicator species (AFIS, 50 species; Table S2). We distinguished alien species, with division into archaeophytes and neophytes according to the national alien plant species checklist (Tokarska-Guzik et al. 2012). We also distinguished guilds of forest species (members of *Querco-Fagetea* Br.-Bl. et Vlieger 1937, *Vaccinio-Piceetea* Br.-Bl. in Br.-Bl. et al. 1939 and *Quercetea roboris-petraeae* Br.-Bl. in R. Tx et al. 1943 nom. mut. classes) and forest edge and ruderal species (*Artemisietea vulgaris* Lohmeyer et al. in R. Tx. 1950, *Epilobietea angustifoli* R. Tx. et Preising in R. Tx. 1950, *Stellarietea mediae* R. Tx. et al. in R. Tx 1950 and *Trifolio-Geranietea* Th. Müller 1962 classes) according to phytosociological review (Ratyńska et al. 2010). We also distinguished AFIS, as a guild of forest specialists, sensitive to forest ecosystem transformation (e.g. Peterken 1974; Orczewska 2009; Dyderski et al. 2017). We distinguished AFIS according to the Dzwonko and Loster (2001) checklist.

We obtained a phylogenetic tree for species present in the study plots from the megatree included in the V.phylo.maker package (Jin and Qian 2019) and we obtained functional traits (Table 2) from LEDA (Kleyer et al. 2008), BIEN (Enquist et al. 2016), BiolFlor (Klotz et al. 2002) and Pladias (Wild et al. 2019) databases, and ecological indicator values from Ellenberg and Leuschner (2010). Due to incomplete trait data, we decided to impute missing data rather than omit them in analyses (see Pyšek et al. 2015) by random forest-based imputation (Penone et al. 2014), implemented in the *missForest* package (Stekhoven and Bühlmann 2012). We enforced the predictive power of imputation models by phylogenetic eigenvectors (Diniz-Filho et al. 1998), obtained using the *PVR* package (Santos 2018). The first 15 phylogenetic eigenvectors covered 59.4% of the variation in phylogenetic distances among species. Normalized root mean squared error of imputed traits was 1.054 for continuous predictors and the proportion of falsely classified categorical variables was 0.401.

Calculation of diversity indices

We investigated the effects of alien tree species on native understory vegetation. We analyzed three aspects of native species diversity–taxonomic, phylogenetic and functional at two levels—alpha (within-site) and beta (among sites). We quantified taxonomic alpha diversity using species richness and Shannon's diversity index, calculated using the vegan package (Oksanen et al. 2018). We quantified phylogenetic diversity using Faith's phylogenetic diversity (PD; i.e. the sum of phylogenetic tree branch lengths, representing all species present in the community) and mean pairwise phylogenetic distance (MPD) between species within the community. We calculated them using the PhyloMeasures package (Tsirogiannis and Sandel 2016). We quantified functional diversity by functional richness (FRic), expressing the quantity of plant functional types present in a community and functional dispersion (FDis), expressing the size of community species traits hypervolume within the functional trait space (Mason et al. 2005; Laliberté and Legendre 2010; Pla et al. 2011). These two indices were calculated using the FD package (Laliberté et al. 2014).

We used Jaccard's dissimilarity index to assess taxonomic, functional and phylogenetic beta diversity, as this metric was the most frequently used in previous studies on biotic homogenization (Olden et al. 2018). Taxonomic beta diversity was based on a presence-absence matrix, functional diversity—on the volume of convex hull intersections in a multidimensional functional space (extracted from principal coordinates analysis from species traits of a Gower dissimilarity matrix) and phylogenetic diversity—on PD; all of these were calculated using the betapart package (Baselga et al. 2018). For each beta diversity index we calculated overall value, nestedness and turnover (Baselga 2010). This allowed us to explain the importance of nestedness (presence of core species) and turnover (species replacement) in shaping dissimilarities among particular forest types.

Data analysis

We analyzed data using R software (v. 3.5.3; R Core Team 2019). We assessed species composition of study plots (using square root transformed data) by detrended correspondence analysis (DCA; Hill and Gauch 1980), implemented in the vegan package (Oksanen et al. 2018). We decided to use DCA as a method dedicated to data across long environmental gradients (over 3 SD units), due to the gradient

Table 2 Traits used in the study, their ranges, variation coefficient (CV) and completeness

Numeric traits	min	max	mean	CV [%]	Completeness [%]
EIV-Light (EIV-L)	1	9	6.1	26.3	96.6
EIV-Moisture (EIV-M)	2	10	5.1	27.6	81.7
EIV-Soil reaction (EIV-SR)	2	9	6.1	27.9	63.0
EIV-Nutrients (EIV-N)	1	9	5.2	40.9	83.6
EIV-Temperature (EIV-T)	2	8	5.6	13.2	67.9
Flowering beginning [months]	1	9	5.2	24.8	97.7
Flowering duration [months]	1	12	3.2	47.9	97.7
Specific leaf area (SLA) [cm^2 g^{-1}]	49.8	899.1	252.1	45.7	93.5
Lead dry mass content (LDMC) [mg g^{-1}]	0.16	509.53	236.39	31.4	85.1
Seed mass (SM) [mg]	0.00	13,737.62	201.13	673.3	93.9
Maximum height (H) [m]	0.03	54.86	6.54	190.9	97.3

Categorical traits	Number of classes	Classes and their frequency	Completeness [%]
Life form	8	Chamaephytes (3.1%), Geophytes (7.6%), Hemicryptophytes (49.6%), Hydrophytes (0.4%), Lianas (5.0%), Phanerophytes (25.2%), Therophytes (9.2%)	100.0
Life strategy	7	C (45.9%), CR (10.2%), CS (16.3%), CSR (22.0%), R (3.3%), S (1.6%), SR (0.8%)	93.9
Pollination mode-insect	2	yes (71.9%), no (28.1%)	95.0
Pollination mode-selfing	2	yes (54.2%), no (45.8%)	95.0
Pollination mode-wind	2	yes (30.9%), no (69.1%)	95.0

detrending procedure included in the analysis. We assessed differences in alpha diversity and richness of particular species guilds using generalized linear mixed-effects models (GLMMs), accounting for dependencies among plots within blocks by the random intercept. We assumed Gaussian distributions of Shannon index, PD, MPD, FRic and FDis and Poisson distribution of species richness. In cases of differences between beta-diversity indices we used linear models. We assessed the impacts of forest type on response variables by ANOVA. Although models could reveal differences among forest types with p-values < 0.05, via Tukey's *posteriori* tests we applied a single-step adjustment of p-values, to account for multiple hypothesis testing. Single-step adjustment decreases the probability of committing Type I error (i.e. rejection of the true null hypothesis), and also accounts for correlations among variables tested (Bretz et al. 2011). We ensured a lack of problems with zero-inflation and overdispersion of

models using tests provided by the DHARMa package (Hartig 2020).

Results

Understory vegetation species composition

Composition of understory vascular plant species revealed the main gradient along DCA1 axis, from the least fertile *P. sylvestris* forests to *P. sylvestris* plantations, *Q. petraea*, *Q. rubra* and *F. sylvatica* forests to the most fertile *Quercus-Acer-Tilia* and *R. pseudoacacia* forests (Fig. 3). Invaded forest types were separated from non-invaded along DCA2 axis (mixed-model ANOVA, numerator df = 1, denominator df = 169.07, $F = 12.872$, $p = 0.0004$). Points representing invaded forest types occurred in the upper part of the ordination space. Most of the AFIS
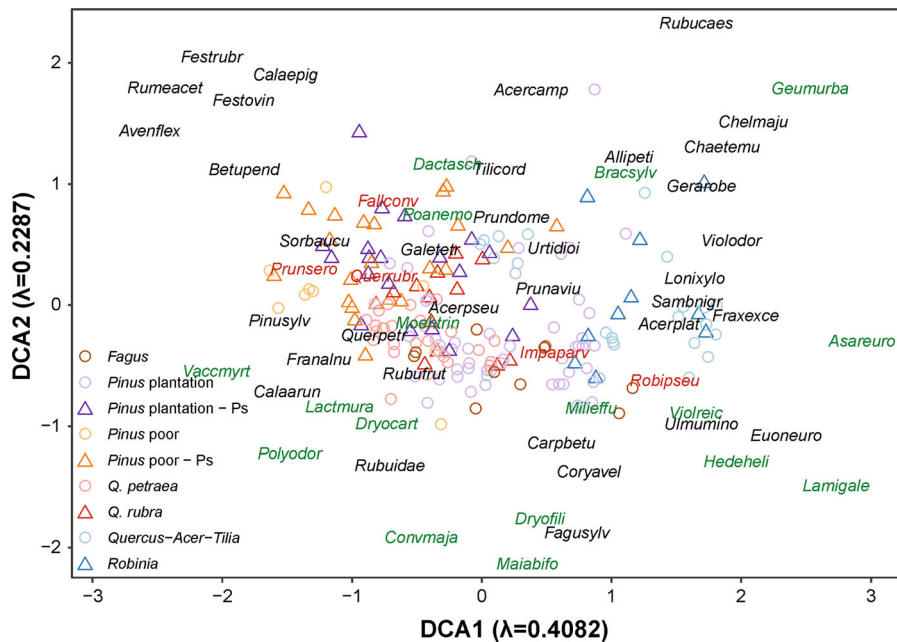
Fig. 3 Detrended Correspondence Analysis of understory species composition on the study plots ($n = 186$). Italicized labels represent species scores and are abbreviations of species names (e.g. *Vaccmyrt = Vaccinium myrtillus*), red label indicates alien species, green label-ancient forest indicator species. Only species with cover sum within the whole dataset > 20% were plotted (57 of 262). Forest types: *Fagus-Fagus sylvatica* dominated forest, *Pinus* plantation-*Pinus sylvestris* forests in fertile sites, *Pinus* plantation-PS-*P. sylvestris* plantation invaded by *Prunus serotina*, *Pinus* poor-*P. sylvestris* forest in poor sites, *Pinus* poor-PS-*P. sylvestris* forest in poor sites invaded by *P. serotina*, *Q. petraea*-acidophilous *Quercus petraea*-dominated forest, *Q. rubra*-*Q. rubra* dominated forests, *Quercus-Acer-Tilia*-*Q. petraea*, *Acer platanoides*, *A. pseudoplatanus*, *Tilia cordata* dominated fertile forest, *Robinia-Robinia pseudoacacia* dominated forest

scores occurred in the lower part of the DCA space, while most of the alien species were in the upper part.

We found the highest number of AFIS and forest species in *Quercus-Acer-Tilia* and *R. pseudoacacia* forests while the lowest—in *F. sylvatica* forests (Table 3, Fig. 4). Non-invaded poor *P. sylvestris* forests hosted 24.8% more forest species than *P. serotina* invaded forests (despite lack of significance

revealed by *posteriori* tests). We also found lower AFIS and forest species numbers in *Q. rubra* than *Q. petraea* forests. We found the highest number of edge and ruderal species in *R. pseudoacacia* forests, 29.8% more than in *Quercus-Acer-Tilia* (despite lack of significance revealed by *posteriori* tests). The lowest number was in *F. sylvatica* and *Q. rubra* forests. We found the most alien species, both archaeophytes and

Table 3 Analysis of variance for ancient forest indicator species (AFIS), forest, edge and ruderal, alien, archaeophyte and neophyte species number in forest types studied, estimated using Poisson GLMMs

| Response	Variable	df	Sum of Squares	Mean Square	F	Pr(> F)	Block random effects SD
AFIS	Forest type	8	443.9000	55.4900	5.7650	< 0.0001	0.253
Forest species	Forest type	8	919.6000	114.9500	9.9310	< 0.0001	0.255
Edge and ruderal species	Forest type	8	1226.0000	153.2900	7.1650	< 0.0001	0.331
Alien species	Forest type	8	265.7000	33.2200	5.6840	< 0.0001	0.269
Neophytes	Forest type	8	154.3000	19.2800	5.6540	< 0.0001	0.241
Archaeophytes	Forest type	8	38.0500	4.7560	4.1520	0.0001	0.512
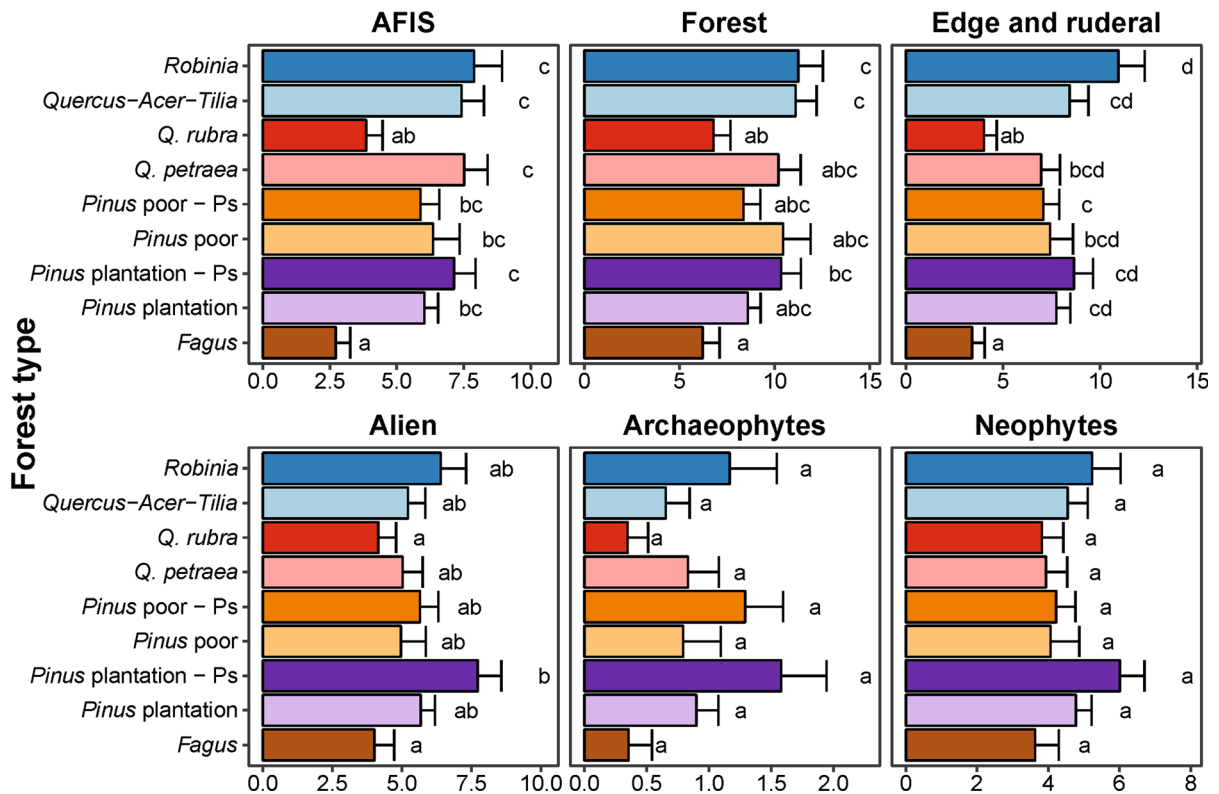
Fig. 4 Mean (+ SE) number of ancient forest indicator species (AFIS), forest, edge and ruderal, alien, archaeophyte and neophyte species in forest types studied (*Fagus*-*Fagus sylvatica* dominated forest, *Pinus* plantation-*Pinus sylvestris* forests in fertile sites, *Pinus* plantation-PS-*P. sylvestris* plantation invaded by *Prunus serotina*, *Pinus* poor-*P. sylvestris* forest in poor sites, *Pinus* poor-PS-*P. sylvestris* forest in poor sites invaded by *P.*

serotina, *Q. petraea*-acidophilous *Quercus petraea*-dominated forest, *Q. rubra*-*Q. rubra* dominated forests, *Quercus-Acer-Tilia*-*Q. petraea*, *Acer platanoides*, *A. pseudoplatanus*, *Tilia cordata* dominated fertile forest, *Robinia*-*Robinia pseudoacacia* dominated forest), estimated using Poisson GLMMs. Letters denote variants that are not different at p = 0.05, according to Tukey *posteriori* tests. For model details see Table 3

neophytes, in *P. serotina* invaded *P. sylvestris* forests. Despite the lack of differences revealed by *posteriori* tests, *P. serotina* invaded *P. sylvestris* plantations had 75.8% more archaeophytes and 25.8% more neophytes than non-invaded plantations. Similarly, *R. pseudoacacia* forests had 78.6% more archaeophytes and 15.1% more neophytes than *Quercus-Acer-Tilia* forests.

Understory vegetation alpha diversity

We found the highest species richness in *R. pseudoacacia* and non-invaded poor *P. sylvestris* forests and *P. serotina* invaded *P. sylvestris* plantations, while the lowest—in *F. sylvatica* and *Q. rubra* forests (Fig. 5, Table 4). *Q. rubra* forests had almost twice lower number of species than *Q. petraea* and *Quercus-Acer-*

Tilia forests, while *P. serotina* invaded *P. sylvestris* plantations had one-fourth more species than non-invaded. We also found statistically insignificant (p > 0.05) but biologically relevant differences: *Quercus-Acer-Tilia* forests had 15% fewer species than *R. pseudoacacia* forests, while non-invaded poor *P. sylvestris* forests had 13% more species than invaded. We found the highest phylogenetic diversity in *R. pseudoacacia* forests and *P. serotina* invaded *P. sylvestris* forests, and the lowest—in *Q. rubra* and *F. sylvatica* forests. We found higher phylogenetic diversity in *Q. petraea* than *Q. rubra* forests and *P. serotina* invaded than non-invaded *P. sylvestris* forests. We also found a statistically insignificant (p > 0.05) but biologically relevant difference in phylogenetic diversity, which was 27% higher in *R. pseudoacacia* than *Quercus-Acer-Tilia* forests. We
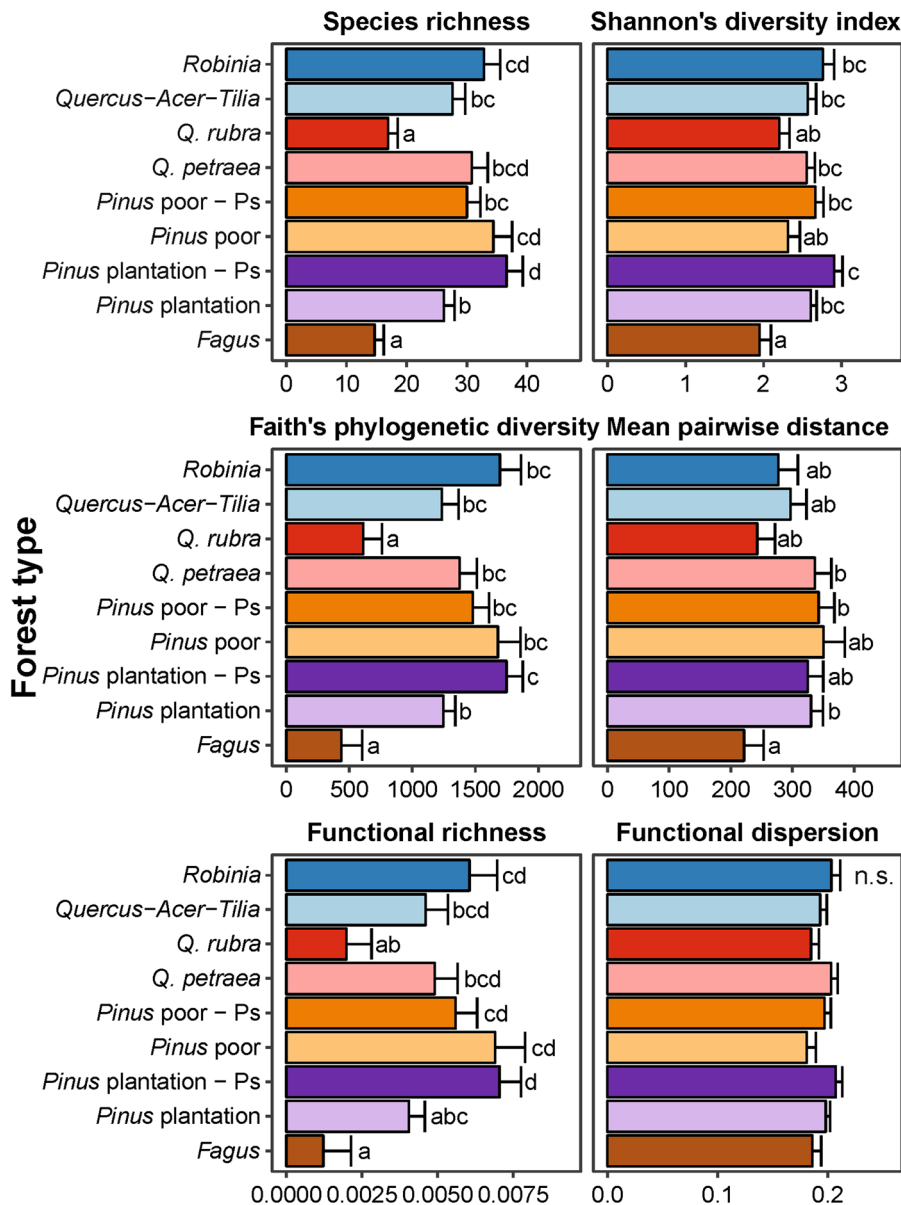
Fig. 5 Mean (+ SE) values of alpha diversity indices in forest types studied (*Fagus-Fagus sylvatica* dominated forest, *Pinus* plantation-*Pinus sylvestris* forests in fertile sites, *Pinus* planta-tion-PS-*P. sylvestris* plantation invaded by *Prunus serotina*, *Pinus* poor-*P. sylvestris* forest in poor sites, *Pinus* poor-PS-*P. sylvestris* forest in poor sites invaded by *P. serotina*, *Q. petraea*-acidophilous *Quercus petraea*-dominated forest, *Q. rubra-Q. rubra* dominated forests, *Quercus-Acer-Tilia-Q. petraea*, *Acer platanoides*, *A. pseudoplatanus*, *Tilia cordata* dominated fertile forest, *Robinia-Robinia pseudoacacia* dominated forest). Let-ters denote variants which are not different at p = 0.05, according to Tukey *posteriori* tests (n.s.-lack of differences between any pair of variants for a particular variable). For model details see Table 4

revealed similar trends in functional richness, while differences between invaded and non-invaded forest types were higher. We did not find biologically relevant differences between invaded and non-invaded forests in species diversity, as well as mean pairwise distance and functional dispersion.

Table 4 Analysis of variance for alpha diversity indices among forest types studied, assessed using linear mixed-effects models (with study plot block as a random intercept)

Response	Variable	df	Sum of Squares	Mean Square	F	Pr(> F)	Block random effects SD
Species richness	Forest type	8	160.3678	20.0460	20.046	< 0.0001	0.265
Shannon diversity index	Forest type	8	8.2356	1.0294	5.720	< 0.0001	0.146
Faith's phylogenetic diversity	Forest type	8	17,473,654.8014	2,184,206.8502	10.821	< 0.0001	286.098
Mean pairwise distance	Forest type	8	184,069.1143	23,008.6393	3.327	0.0014	62.986
Functional dispersion	Forest type	8	0.0086	0.0011	1.978	0.0525	0.008
Functional richness	Forest type	8	0.0003	0.0000	6.703	< 0.0001	0.002

Understory vegetation beta diversity

We found the highest taxonomic and phylogenetic beta-diversity in *F. sylvatica* forests and the lowest—in *P. serotina* invaded *P. sylvestris* plantations and *R. pseudoacacia* forests (Fig. 6, Table 5). For functional beta diversity we found the highest values in *F. sylvatica* and *Q. rubra* forests, and the lowest—in *P. serotina* invaded *P. sylvestris* plantations. *Q. rubra* forests had higher functional and phylogenetic beta diversity than *Q. petraea* forests due to higher nestedness, while we did not find such a pattern in taxonomic beta diversity. *R. pseudoacacia* forests had lower taxonomic and phylogenetic beta diversity, but similar functional beta diversity as *Quercus-Acer-Tilia* forests. Here differences resulted from higher taxonomic and phylogenetic turnover, with the same level of nestedness. *P. serotina* invaded poor *P. sylvestris* forests had lower functional beta diversity than non-invaded poor *P. sylvestris* forests, due to lower nestedness. We did not confirm differences for taxonomic and phylogenetic beta diversity. In contrast, invaded *P. sylvestris* plantations had lower taxonomic, functional and phylogenetic beta diversity than non-invaded *P. sylvestris* plantations. In all cases non-invaded *P. sylvestris* plantations had higher nestedness than invaded ones.

Discussion

Impacts are mediated by influences of invasive trees on resource availability

Impacts of the invasive tree species studied differed among species and habitats. We found the lowest reduction of alpha diversity and specialists in *Q. rubra* forests, while we found no reduction in *R. pseudoacacia* forests, compared to mature native forests. In poor *P. sylvestris* forests, *P. serotina* invasion decreased alpha diversity, while in *P. sylvestris* plantations we did not find such a pattern. This may suggest that impacts of invasive trees on understory alpha diversity are more severe where resources are more limiting—such as light in *Q. rubra* forests and soil nutrients in poor *P. sylvestris* forests. This explains the high consistency among studies revealing negative effects of *Q. rubra* on understory vegetation (Marozas et al. 2009; Woziwoda et al. 2014; Gentili et al. 2019) and some results revealing no impacts (Verheyen et al. 2007; Chabrerie et al. 2010; Gentili et al. 2019) of *P. serotina*. Moreover, studies reported that *P. serotina* decreased understory plant diversity on less fertile sites resembling poor *P. sylvestris* forests from this study (Godefroid et al. 2005; Halarewicz and Żołnierz 2014). Halarewicz (2012) also found a lower effect size of *P. serotina* impacts on species richness in fertile than in poor *P. sylvestris* forests. Therefore, the reference ecosystem influences
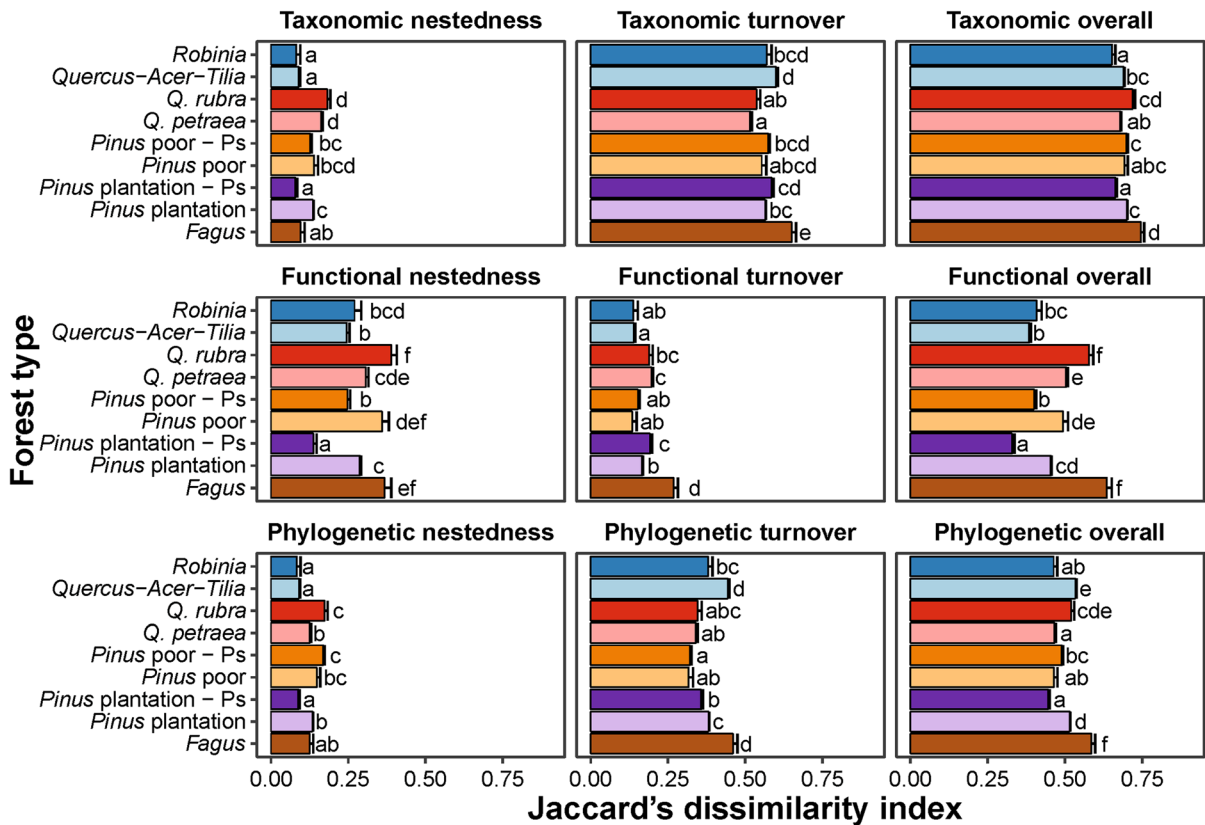
Fig. 6 Mean (+ SE) turnover, nestedness and overall beta diversity in forest types studied (*Fagus-Fagus sylvatica* dominated forest, *Pinus* plantation-*Pinus sylvestris* forests in fertile sites, *Pinus* plantation-PS-*P. sylvestris* plantation invaded by *Prunus serotina*, *Pinus* poor-*P. sylvestris* forest in poor sites, *Pinus* poor-PS-*P. sylvestris* forest in poor sites invaded by *P. serotina*, *Q. petraea*-acidophilous *Quercus petraea*-dominated forest, *Q. rubra-Q. rubra* dominated forests, *Quercus-Acer-Tilia-Q. petraea*, *Acer platanoides*, *A. pseudoplatanus*, *Tilia cordata* dominated fertile forest, *Robinia-Robinia pseudoacacia* dominated forest). Letters denote variants that are not different at $p = 0.05$, according to Tukey *posteriori* tests. For model details see Table 5

the effect of *P. serotina* invasion on alpha diversity metrics. In contrast, *R. pseudoacacia* impacts were not due to decreased light availability, but rather due to nitrogen fixation and increased soil nitrogen availability (Rice et al. 2004), resulting in increasing alpha diversity or no impacts, similar to other studies (Sitzia et al. 2012; Hejda et al. 2017; Gentili et al. 2019). However, still other studies revealed decreases of species diversity by *R. pseudoacacia*, in comparison with *Betula pendula* urban forests (Kowarik et al. 2019), *Q. cerris* and *Q. pubescens* thermophilous forests (Lazzaro et al. 2018) or shrublands on abandoned fields in China (Kou et al. 2016). Therefore, although our results suggested increased alpha diversity in *R. pseudoacacia* forests, it can only be compared with mature native temperate forests in

Europe, as comparisons with other reference ecosystems (see above) are in contrast.

Eco-evolutionary novelty does not increase impacts of invasive trees

Since Darwin's (1859) observations, numerous theories in invasion ecology assumed that success or impacts of invasive species depend on the phylogenetic or functional similarity of alien and native species (Ricciardi and Atkinson 2004; Enders et al. 2020). Earlier studies revealed higher impacts of alien species less similar to native species (Ricciardi and Atkinson 2004), but impacts of alien species also depend on species quantity in the ecosystems (Kumschick et al. 2015). Alien tree species are more

Table 5 Analysis of variance for beta diversity indices among forest types studied

Response	Variable	df	Sum of squares	Mean square	F	Pr(> F)
Taxonomic nestedness	Forest type	8	3.301	0.413	29.836	< 0.0001
	Residuals	5083	70.305	0.014		
Taxonomic turnover	Forest type	8	3.068	0.384	19.241	< 0.0001
	Residuals	5083	101.318	0.020		
Taxonomic overall	Forest type	8	1.104	0.138	13.740	< 0.0001
	Residuals	5083	51.042	0.010		
Functional nestedness	Forest type	8	12.229	1.529	34.938	< 0.0001
	Residuals	5083	222.397	0.044		
Functional turnover	Forest type	8	2.435	0.304	16.483	< 0.0001
	Residuals	5083	93.878	0.018		
Functional overall	Forest type	8	16.343	2.043	86.742	< 0.0001
	Residuals	5083	119.712	0.024		
Phylogenetic nestedness	Forest type	8	2.841	0.355	29.095	< 0.0001
	Residuals	5083	62.040	0.012		
Phylogenetic turnover	Forest type	8	6.075	0.759	38.912	< 0.0001
	Residuals	5083	99.201	0.020		
Phylogenetic overall	Forest type	8	4.065	0.508	41.606	< 0.0001
	Residuals	5083	62.073	0.012		

abundant in sites occupied by functionally similar species (Sande et al. 2020). Therefore, both of these contradictory findings could be valid. We expected *R. pseudoacacia* to cause the highest decrease of alpha diversity, compared to mature native forests. In temperate European forests this species is more phylogenetically distinct (no native congenerics, in contrast to *P. serotina* and *Q. rubra*). Its functional distinction is lower—there are functionally similar shrub species (e.g. nitrogen-fixing legume *Cytisus scoparius*) and tree species which also fix nitrogen (e.g. *Alnus glutinosa*). Reference to mature forest ecosystems here does not allow conclusions about the effects of *R. pseudoacacia* in early-successional stages, where it can be more functionally and phylogenetically similar to native species. We also expected the lowest impact of *Q. rubra*, which is both phylogenetically and functionally similar to native species (*Q. petraea* and *F. sylvatica*). Although biodiversity metrics of *Q. rubra* understory were similar to *F. sylvatica* forests, their composition was more similar to *Q. petraea* and *P. sylvestris* forests. However, it differed from *Quercus-Acer-Tilia* forests, similarly as in Central Poland (Woziwoda et al. 2014) and

Lithuania (Marozas et al. 2009). In the case of *P. serotina* we could predict low impacts according to the presence of both phylogenetically related (*P. padus*, *P. avium*) and functionally similar (e.g. *Sorbus aucuparia*, *Frangula alnus*) species. However, we found a decrease of alpha diversity in *P. serotina* invaded forests only in poor *P. sylvestris* forests, where *P. serotina* congenerics do not occur and functionally similar species are sparsely distributed. In contrast, *P. sylvestris* plantations are usually colonized by numerous shrubs, including *P. avium* and *S. aucuparia*, forming dense shrub layers (Zerbe and Wirth 2006). This only partially supports the theory of eco-evolutionary naivety (Ricciardi and Atkinson 2004; Enders et al. 2020). Our results rather showed that influences of alien tree species on biodiversity are mediated by their abundance (Kumschick et al. 2015), which is positively correlated with functional similarity to native species (Sande et al. 2020).

More alien species in invaded forests—invasional meltdown or biotic acceptance?

We found higher numbers of alien species in *R. pseudoacacia* and *P. serotina* invaded *P. sylvestris* forests than in non-invaded and *Q. rubra* forests. These findings are in line with previous studies, revealing higher or the same alien species richness (e.g. Von Holle et al. 2013; Halarewicz and Żołnierz 2014; Slabejová et al. 2019). The one exception was a study comparing *R. pseudoacacia* forests with *Betula pendula* forests in Berlin (Trentanovi et al. 2013). Some variation in the number of alien species may result from the spread of natural regeneration of the invasive tree species studied, which successfully colonized adjacent forests (Dyderski and Jagodziński 2018). Also, among herbaceous species, one of the most widespread is the neophyte *Impatiens parviflora*, occurring in various types of ecosystems across Central Europe (Chmura 2004; Chmura and Sierka 2007; Godefroid and Koedam 2010). These two phenomena blur the effects of alien species facilitation of secondary invasions, known as invasional meltdown (Simberloff and Von Holle 1999; Simberloff 2006). Higher alien species richness, compared to mature native forests, may be connected with habitat modification—increased nutrient availability by *P. serotina* (Aerts et al. 2017) and *R. pseudoacacia* (Rice et al. 2004), due to high decomposition rate of their leaf litter (Horodecki and Jagodziński 2017). Moreover, *P. sylvestris* plantations are more invasible (Zerbe and Wirth 2006), due to soil acidification (Augusto et al. 2002) and higher light availability, connected with low leaf area per unit of basal area (Dyderski and Jagodziński 2019b). Forest types with high alien species richness were also rich in native species, supporting the biotic acceptance theory (Stohlgren et al. 1999, 2006; Dyderski et al. 2015), and also connected with resource availability.

Biotic homogenization—invasive trees decreased beta diversity

We found that *R. pseudoacacia* decreased taxonomic and phylogenetic beta diversity, compared to mature native forests. Previous studies showed an increase (Kou et al. 2016), decrease (Šibíková et al. 2019) and no impacts (Sitzia et al. 2012; Trentanovi et al. 2013)

of *R. pseudoacacia* on taxonomic beta diversity. Our study is in line with findings from Southern Europe (Šibíková et al. 2019), which also compared *R. pseudoacacia* forests with *Quercus-Acer-Tilia* forests. Other studies compared effects of *R. pseudoacacia* on other reference ecosystems—e.g. early-successional post-agricultural forests (Sitzia et al. 2012; Kou et al. 2016) or urban forests (Trentanovi et al. 2013). In *P. sylvestris* plantations we confirmed lower taxonomic, functional and phylogenetic beta diversity in *P. serotina* invaded forests. In contrast, in poor *P. sylvestris* forests we found only lower functional beta diversity in invaded than non-invaded forests. Both taxonomic and phylogenetic beta diversity were more driven by species turnover than nestedness. This suggests that the main driver of beta-diversity was the ability to host random elements of species composition rather than the presence of core elements of understory vegetation (Baselga 2010). This may be connected with vegetation continuity (Holeksa and Woźniak 2005; Austin 2013) and suggests low impacts of invasive tree species on individualistic understory plant species responses. However, functional beta diversity was more driven by nestedness than the turnover in all forest types, except *P. serotina* invaded *P. sylvestris* plantations. This indicates that particular forest types host a core of functionally similar understory species, which are different in terms of taxonomic affiliation and evolutionary history. This suggests functional filtering of understory plant species, connected with resource availability.

In contrast to other invasive tree species studied, we found higher values of all beta-diversity metrics in *Q. rubra* forests. High beta diversity of *Q. rubra* forests is connected with high turnover and lack of constant species, similar to *F. sylvatica* forests. These two types are located in the middle part of the ordination space and characterized by low to medium soil fertility and low light availability. These two filters reduce the number of species and their abundance, therefore most of the species are transient from adjacent forests. Thus, low alpha diversity and high species turnover lead to high beta diversity, but low conservation values.

Conclusions

Our study demonstrated how the three invasive tree species most widespread in European forests affected

alpha and beta diversity of understory vegetation, in comparison to mature native forests. Due to using mature native forests as reference ecosystems, our conclusions cannot inform impacts in other types of ecosystems invaded by the tree species studied, e.g. shrublands or early-successional forests. We provided the first assessment of all three facets of diversity (taxonomic, functional and phylogenetic) for the species studied, broadening the understanding of invasive tree impacts on plant diversity. We proved that invaded forests differ from non-invaded forests in species composition, but did not always have decreased alpha and beta diversity. Influence on understory vegetation diversity depended on a particular invasive species ability for habitat transformation—we found the highest decrease of alpha diversity in *Q. rubra* forests, with low levels of soil nutrients and light availability, while we found increases or no effects in nutrient-rich *R. pseudoacacia* forests. This also explains the different patterns of *P. serotina* impacts in nutrient-poor and rich *P. sylvestris* forests. Both *P. serotina* and *R. pseudoacacia* decreased beta diversity, compared to mature native forests. Due to the high importance of species turnover in shaping taxonomic and phylogenetic beta diversity and the high importance of nestedness in shaping functional beta diversity, these invasive species probably limited the number of random species shaping the regional pool. In contrast, *Q. rubra* forests had higher beta diversity than mature native forests, due to low alpha diversity and high turnover of species, connected with low resource levels.

Impacts of particular invasive species depended on the reference ecosystem properties, which is a source of inconsistency in previous studies, which usually referred to single native ecosystem types. In our case, we referred to the mature native forest ecosystems, which have naturally low alpha-diversity in comparison to early-successional stages. However, these forests contain rare and specialized species, the decline of which contributes to regional and global biodiversity reduction. In terms of global effects on biodiversity, this impact can be a more important effect of the alien tree species studied than decreases of alpha-diversity metrics.

Compliance with ethical standards

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