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Functional traits of acquisitive invasive woody species differ from conservative invasive and native species

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Abstract

One of the most important sources of invasiveness is species' functional traits and their variability. However, there are still few studies on invasive tree species traits conducted along resource gradients that allow for a comparison of acquisitive and conservative strategies. We aimed to assess the differences in trait variation among native, alien conservative and alien acquisitive tree species along resource availability gradients (soil fertility and light availability) and to assess the traits variability of the species studied along resources availability gradients. Our study compared invasive tree species in Europe (*Prunus serotina* Ehrh., *Quercus rubra* L. and *Robinia pseudoacacia* L.) with their native competitors (*Acer pseudoplatanus* L., *A. platanoides* L., *Quercus petraea* (Matt.) Liebl. and *Fagus sylvatica* L.). The study was conducted on 1329 seedlings and saplings collected in a system of 372 study plots in W Poland. For each individual we assessed leaf, stem and root mass ratios, total biomass, leaf area ratio, specific leaf area and projected leaf area. Two invasive species (*P. serotina* and *R. pseudoacacia*) represented a more acquisitive strategy than native species – along litter pH and light availability gradients these species had higher leaf mass fraction, specific leaf area and leaf area ratio. In contrast, *Q. rubra* had the highest total biomass and root mass fraction. Alien species usually had higher coefficients of variation of studied traits. This suggests that relatively high projected leaf area, as a way of filling space and outcompeting native species, may be reached in two ways – biomass allocation to leaves and control of leaf morphology or by overall growth rate. High variability of invasive species traits also suggests randomness in seedling survival, which similarly to the neutral theory of invasion, highlights the necessity of including randomness in modelling biological invasions.

Keywords

Prunus serotina, *Quercus rubra*, *Robinia pseudoacacia*, biomass, natural regeneration, functional traits

Introduction

The success of invasive plant species is connected to three main groups of factors: propagule pressure, habitat invasibility and species invasiveness. Interactions among them determine the successful spread of alien species in their exotic ranges (Davis et al. 2005; Jeschke 2014; Ricciardi et al. 2017). Propagule pressure shapes the arrival of new specimens and depends on distance to the propagule source (e.g. Jagodziński et al. 2015), propagule quantity and quality (Sinclair and Arnott 2015). Habitat invasibility expresses ecosystem vulnerability to invasion (Alpert et al. 2000; Davis et al. 2005). Species invasiveness is defined by life history traits determining ability to colonize new areas (Alpert et al. 2000; Grotkopp et al. 2010; Pyšek et al. 2014).

Most studies highlight several traits responsible for effective reproduction and spread (Pyšek et al. 2015; Capinha et al. 2015; Bonilla and Pringle 2015), as well as growth rate or traits connected with resource acquisition (Grotkopp et al. 2010; Tecco et al. 2010; te Beest et al. 2015). One of the most important features of invasive species concerns adaptation to new habitat conditions – enemies or levels of resources (Funk 2008; Jeschke 2014).

Species fitness is the ability to reach ecological success (survive, grow and reproduce) in a particular type of environment (Davidson et al. 2011). One measure of adaptation is phenotypic plasticity. This index reflects the difference in particular species traits within two levels of resources, related to the maximum trait value (Valladares et al. 2000). Studies of invasive species usually reported higher phenotypic plasticity of alien species in comparison with their native relatives (e.g. Davidson et al. 2011; Godoy et al. 2011; Paquette et al. 2012), which is claimed to be responsible for the effective spread of invasive species (Richards et al. 2006). Experimental design allows for a reduction of the number of factors studied and unbiased estimation of their influence, but does not reflect interactions of real factors in the field. However, field trials in natural conditions do not allow for determination of phenotypic plasticity, but only level of trait variability, which depends on both phenotype and genotype. Although few studies have assessed functional traits in the field (e.g. Kuehne et al. 2014; Lieurance and Landsbergen 2016; Heberling and Mason 2018) most of them covered few habitat types and treated resource levels discretely. For that reason there is a lack of gradient studies examining trait responses in multiple comparable sites along major environmental gradients (Hulme and Bernard-Verdier 2018). Moreover, studies based on phylogenetically-related pairs of species do not reflect real relationships between species in ecosystems (Hulme 2008).

Invasive species usually represent higher values of traits connected with size, growth rate, leaf-area allocation and shoot allocation (van Kleunen et al. 2010). Tecco et al. (2010) found two general trends of variation in trait syndromes: acquisitive (high SLA) and conservative (low SLA). In the case of woody species, alien species had a more acquisitive growth strategy in comparison with native species. This strategy was called 'try harder' – alien plants exhibited higher values of traits responsible for resource acquisition than their native competitors. For example, higher SLA than those of native savannah species is responsible for the success of invasive *Chromolaena odorata* (te Beest et al. 2015).

In contrast, Grotkopp et al. (2010) found lack of differences in acquisitive traits between invasive and non-invasive species, but instead found differences in growth and assimilation rates. However, there are still few studies on invasive tree species conducted along resource gradients that allow for a comparison of acquisitive and conservative strategies.

We aimed to assess the differences in trait variation among native alien tree species and traits variability along resource availability gradients (i.e. soil fertility, approximated by litter pH, and light availability). We hypothesized that: (1) similarly to the observations of Tecco et al. (2010), invasive species will express a more acquisitive set of functional traits than their native competitors; (2) according to previous studies (e.g. Richards et al. 2006; Davidson et al. 2011; Godoy et al. 2011) invasive species will exhibit higher variation of the traits studied and (3) according to 'try hard' strategy typical of alien species (Tecco et al. 2010), alien species will be more responsive to environmental gradients of resources availability.

Methods

Species studied

We studied the three alien tree species that are most frequent in European woodlands: *Prunus serotina* Ehrh., *Quercus rubra* L. and *Robinia pseudoacacia* L. (Wagner et al. 2017). These species came from eastern North America and have been introduced via forestry, in the 18th, 19th and 17th centuries, respectively (Muys et al. 1992; Cierjacks et al. 2013; Woziwoda et al. 2014). All the species strongly modify invaded habitats by influencing leaf litter decomposition (Dobrylovská 2001; Horodecki and Jagodziński 2017), nutrient cycling (Rice et al. 2004; Aerts et al. 2017) and light availability (Knight et al. 2008; Chmura 2013; Jagodziński et al. 2018). *R. pseudoacacia* is dispersed by wind (Cierjacks et al. 2013; Vítková et al. 2017), *P. serotina* by birds (Pairon et al. 2006; Jagodziński et al. 2015; Dylewski et al. 2017) and *Q. rubra* by birds and rodents (Myczko et al. 2014; Bieberich et al. 2016). *P. serotina* and *R. pseudoacacia* are mid-successional species while *Q. rubra* – late-successional, which is manifested in their abundance and disturbance responses (Dyderski et al. 2018). For comparison we chose the four native species most frequent within study plots: *Acer pseudoplatanus* L., *A. platanoides* L., *Quercus petraea* (Matt.) Liebl. and *Fagus sylvatica* L. In a preliminary inventory of natural regeneration in 2015 these species were found in 80.1%, 46.5%, 68.5% and 34.9% of 372 study plots, respectively, in comparison with *P. serotina* (59.9%), *Q. rubra* (44.6%) and *R. pseudoacacia* (23.6%). The native species chosen were not phylogenetically related to the invasive species, but are their most frequent competitors in the regeneration layer. *A. platanoides* and *A. pseudoplatanus* are mid-successional species dispersed by wind while *F. sylvatica* and *Q. petraea* are late-successional species dispersed by birds and rodents. Despite the affiliation of the species being studied in successional stages, the pattern of species co-occurrence did not follow the division into early-, mid- and late-successional species (Suppl. material 1: Fig. S1).

Study area

We conducted our study in the Wielkopolski National Park (WNP; W Poland; 52°16'N, 16°48'E; 7584 ha). The main aim of conservation in WNP is to preserve a valuable post-glacial landscape, including valleys, moraine hills and lakes. The climate in WPN is temperate, transitional between oceanic and continental. Mean annual temperature in Poznań (c.a. 15 km from WNP) was 8.4 °C and mean annual precipitation was 521 mm for the years 1951–2010. Dominant soil types in the study area are luvisols (47%) and brunic and haplic soils (30%), while podzols constitute only 7% (Nowak et al. 2000). The most frequent plant associations are *Galio sylvatici-Carpinetum* (fertile broadleaved forest dominated by *Quercus*, *Carpinus* and *Tilia*), *Calamagrostio arundinaceae-Quercetum* (acidophilous forest with *Q. petraea*) and *Querco roboris-Pinetum* (mixed *Quercus-Pinus* forest). However, there are small vegetation patches of both fertile riparian forests (*Fraxino-Alnetum*, *Querco-Ulmetum minoris*) and poor coniferous forests (*Leucobryo-Pinetum*). Most of the fertile sites were planted with *Pinus sylvestris* before the national park establishment in 1957 (Nowak et al. 2000). Moreover, WNP is the national park with the highest richness of alien woody taxa in Poland (158; Purcel 2009; Gazda and Szwagrzyk 2016). There are pure stands of alien species surrounded by large areas of forest ecosystems with different levels of disturbances and human impacts. This makes WNP an excellent place to test hypotheses about the impact of disturbances on the ecological success of invasive species.

Study design

The study design covers a set of 378 plots (100 m^2) arranged in 21 blocks: nine for *Q. rubra* and six for *P. serotina* and *R. pseudoacacia* with the central part of each block located in a monoculture stand of invasive species (Dyderski and Jagodziński 2018a, b). Because *P. serotina* occurs only as an admixture in tree stands, as central parts we used tree stands with high densities of fruiting *P. serotina* trees in the shrub layer. In the center of each block we established a pair of study plots. Then, we established additional pairs of study plots along each of the four sides (N, S, E, and W) nearly outside the stand, at the invasion edge (the border between crowns of the invasive species monoculture and the surrounding trees; Rodríguez et al. 2017). The next four pairs were located 30 m from the invasion edge. This design generated 18 study plots within each block. Six study plots were excluded, as due to their systematic distribution, these plots were located outside the forest vegetation. Thus, the final number of plots was n=372. Study plots represented most of the vegetation types occurring in Wielkopolski National Park and wide gradients of resource availability: litter pH ranging from 3.83 to 6.44 and light availability ranging from 0.7 to 25.1% of the open sky (see details of measurements below). The variability of microsites conditions within the plot system (Dyderski and Jagodziński 2018a, b), was accounted for in the study design by including the 'plot' term as a random effect in mixed models (Roberts et al. 2017).

Data collection

In July 2017 we destructively harvested sample trees: seedlings (defined as individuals germinated in a particular year) and saplings (defined as individuals at least one year old and with height < 0.5 m). We divided natural regeneration into seedlings and saplings due to low seedlings survival (Beckage and Clark 2003; Knight et al. 2008; Canham and Murphy 2016), supply of carbohydrates stored in seed (Curt et al. 2005; Ziegenhagen and Kausch 1995) and differences in morphology affecting the functional traits studied (Cierjacks et al. 2013; Annighöfer et al. 2016). We surveyed an area within a 5 m wide buffer around each plot pair and we randomly selected up to five specimens for each species. The number of harvested plants was proportional to the available number of specimens and species densities within plots. We did not collect heavily damaged and browsed plants, unless there were no alternative specimens in the area examined. This accounted for the joint effects of lower growth and resistance to herbivory in suboptimal sites (Dyderski and Jagodziński 2018b). Field study within uncontrolled growth conditions resulted in unequal numbers of sample trees per species: 75 saplings and 48 seedlings of *A. platanoides*, 91 and 341 of *A. pseudoplatanus*, 23 and 59 of *F. sylvatica*, 141 and 191 of *P. serotina*, 29 and 78 of *Q. petraea*, 56 and 71 of *Q. rubra* and 37 and 89 of *R. pseudoacacia*. This inequality was an effect of unequal distributions of natural regeneration of the species within the study plots (Dyderski and Jagodziński 2018a, b). We dug each sample tree, and then carefully cleaned and divided it into roots, stems with branches and leaves. We did not include acorns which were still attached to *Q. rubra* and *Q. petraea* seedlings in the total biomass. We excluded from the dataset 14 *P. serotina* and 23 *R. pseudoacacia* saplings which had root suckers.

After separation, all sample tree biomass components were packed into envelopes, unfolded and transported into the laboratory. Leaves which were suitable for scanning, according to Cornelissen et al. (2003), were dried separately in a special press. All material was dried in an oven with forced air circulation at 65 °C (UN 750 and ULE 600, Memmert GmbH+Co.KG, Germany), to a constant mass. All biomass components were weighed using a BP 210 S (Sartorius, Göttingen, Germany) with an accuracy of 0.001 g. Leaves were scanned using WinFOLIA 2013 PRO software (Regent Instruments Inc., Quebec, Canada) to measure their leaf area. From the area and leaf dry biomass of scanned leaves, specific leaf area (SLA) was calculated, as leaf area divided by leaf mass. We also calculated leaf area ratio (LAR) as a ratio of projected leaf area (PLA; SLA multiplied by total leaf biomass) and TB (total biomass), as well as leaf mass fraction (lmf), stem mass fraction (smf) and root mass fraction (rmf). We analyzed traits of biomass allocation (lmf, smf, rmf) expressed as plant investment in particular organs – acquisition of limiting resources (Jagodziński and Oleksyn 2009; Poorter et al. 2015; Lieurance and Landsbergen 2016). TB was used as an overall plant fitness measure reflecting space filled by the species, and is also claimed to be a good measure of plant fitness (Younginger et al. 2017). We chose three leaf traits: SLA reflecting resource use efficiency within foliage (Wright et al. 2004; Díaz et al. 2016), PLA reflecting filling of space by foliage (Jagodziński et al. 2016) and LAR as a measure of whole plant investment in foliage efficiency. These factors are known to vary across soil fertility and light availability gradients.

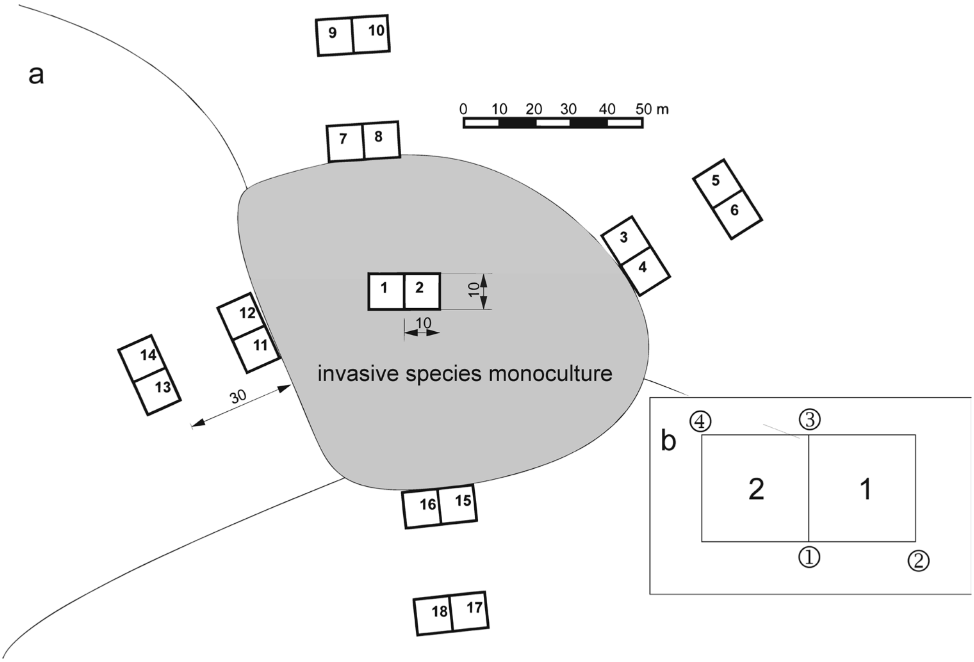

Figure 1. Study design: **a** scheme for a block of experimental plots in the field (each of 21 blocks is a set of 18 100 m^2 square plots; Dyderski and Jagodziński 2018a, b) **b** scheme for litter collection (circles with numbers 1–4 are 0.16 m^2 litter samples, collected in March 2017).

To characterize environmental gradients we used light availability and litter pH. We measured light availability as canopy openness index (diffuse non-interceptance; DIFN) using an LAI-2200 plant canopy analyzer (Li-Cor Inc., Lincoln, NE, USA). For each plot pair we recorded eight series of ten samples (four for each single plot) in August 2016. Although light availability was not measured in the year of harvest, we found low differences in light availability expressed by Ellenberg's ecological indicator community-weighted mean values between 2016 and 2017. The differences ranged from 0.00 to 1.37, with an average of 0.23±0.02, in nine-degree scale, which is within the range of interannual species turnover, as the highest changes we found in plots with low number of species. Thus, we assumed that light availability did not change between 2016 and 2017 significantly. In March 2017 we collected four samples of leaf litter from circular plots (0.16 m^2; Fig 1b). Litter pH was assessed using an electronic pH-meter in distilled water solution after 24 hours. We used litter pH as a proxy for nutrient cycling rates and soil acidity in forest ecosystems (Bigelow and Canham 2002). However, as this variable explains only part of the variability in soil fertility, we encourage caution in interpretation, as one component of soil fertility may be masked by another, not related to litter pH, e.g. nitrogen:phosphorus ratio.

Data analysis

Our study design covered three invasive species with different biologies and we did not choose native species as phylogenetically-related pairs, but rather the most frequent competitors. For that reason we did not test specific alien-native species pairs but we compared each alien species to each native. For comparison of mean trait values of species we used one-way mixed-effects ANOVA followed by a Tukey *post hoc* test, implemented in the *multcomp::glht()* function. In this model we treated species as a fixed effect and plot as a random effect, to account for plot-specific effects, such as microsite variability and other unknown effects. Mixed models were developed using the *lmerTest::lmer()* function (Bates et al. 2015; Kuznetsova et al. 2017). To assess differences between saplings and seedlings within each species-trait combinations we used t-tests implemented in *stats::t.test()* function. Due to multi-species comparisons we decided not to apply any restrictions on p-values following Moran (2003).

To compare variability of the traits studied we assessed differences in trait coefficients of variation (CV) between two species using Krishnamoorthy and Lee's (2014) modified signed-likelihood ratio test (M-SLR test) implemented in the *cvequality::mslr_test()* function (Marwick and Krishnamoorthy 2016). This test has lower rates of type I error and more power across a range of conditions than the widely used (e.g. Funk 2008; Paquette et al. 2012) asymptotic test of Feltz and Miller (1996). Moreover, the M-SLR test allows for uneven sample numbers, which is necessary for our study design.

To assess the differences among species across resources availability gradients we used random forest algorithm (Breiman 2001). This method has a good performance in case of non-normal distributions of studied parameters, accounts for interaction between correlated predictors and has also a high predictive power. Its potential drawback might be an overfitting, which limits potential model transferability. To stabilize variance and avoid the influence of different units of predictors, prior to analyses we centered and scaled predictors, i.e. we subtracted mean values and divided by SD. To decrease overfitting we used repeated cross-validation by randomly splitting a dataset into training and validation sets within each iteration of model building (10 repeats 10 times) in the *caret::train()* function (Kuhn 2008). Within each iteration 75% of the dataset was used as training set and 25% – as validation set. To conclude about models output we provided information about variable importance, expressed as drop-out loss, i.e. loss in model RMSE when a particular variable is perturbed within the data table. Drop-out loss, similarly to RMSE, is expressed in the units of dependent variable. To show differences between species studied and interactions between species and resource availability we used partial dependence plots. These plots show output predicted for each observation, assuming constant value of other variables. As a constant value algorithm inputs mean values of parameters. These analyses were conducted using DALEX and ceterisParibus packages (Biecek 2018a, b). All analyses were conducted using R software (R Core Team 2018).

Results

Differences in trait values among species

Analysis of mean values of traits revealed statistically significant differences among the species studied ($p<0.001$; Fig. 2, Suppl. material 1: Table S1). Two species (*Q. rubra* and *Q. petraea*) had the highest TB and *Q. rubra* had the highest PLA. Two invasive species (*P. serotina* and *R. pseudoacacia*) had the highest SLA, LAR and leaf mass fraction and the lowest root mass fraction. Comparing seedlings and saplings we found statistically significant ($p<0.05$) differences in 38 of 47 species-trait pairs studied (Fig. 2, Suppl. material 1: Table S2). We did not find statistically significant differences ($p>0.05$) in the case of *Q. petraea* and *R. pseudoacacia* leaf mass fraction, *F. sylvatica* and *Q. rubra* PLA, *Q. petraea* and *Q. rubra* root mass fraction, *A. platanoides* and *F. sylvatica* seedlings SLA and *R. pseudoacacia* TB.

Coefficients of variation of traits

Analysis of trait CVs within species pairs in most cases revealed statistically significant differences in CVs between species (Fig. 3). Within native species *F. sylvatica* usually had higher CVs of functional traits than other native species and did not, statistically, differ significantly in any CV with *A. platanoides*. *P. serotina* and *R. pseudoacacia* had significantly higher CVs statistically of most traits studied than native species. The exceptions were higher CV of smf in *A. pseudoplatanus* saplings and LAR in *A. pseudoplatanus* seedlings than *P. serotina*, and higher TB CVs for *Acer* spp. than *R. pseudoacacia*. Moreover, all native species saplings had higher CVs of PLA than *R. pseudoacacia* saplings.

Trait variability among species and along resource availability gradients

Random forest models revealed that in all traits except SLA in case of seedlings species identity was the most important factor shaping trait values (Table 1). In general, SLA, LAR and lmf decreased with increasing DIFN, however differences among species studied were higher than differences along resource availability gradients (Figs 4, 5). We noted similar traits reaction to soil pH, while in the highest range of pH (over 6.0), SLA, LAR and lmf decrease was higher than in pH up to 6.0. Root mass fraction increased with increasing DIFN but decreased with increasing pH. TB increased with both increasing DIFN and pH. In terms of leaf investment (SLA, LAR, lmf) *R. pseudoacacia* presented the highest values across both DIFN and pH gradients, *P. serotina* had intermediate SLA and LAR, in comparison with native species. *Q. rubra* had the lowest values, while it had the highest total biomass and PLA, as well as similar rmf as native *Q. petraea*.

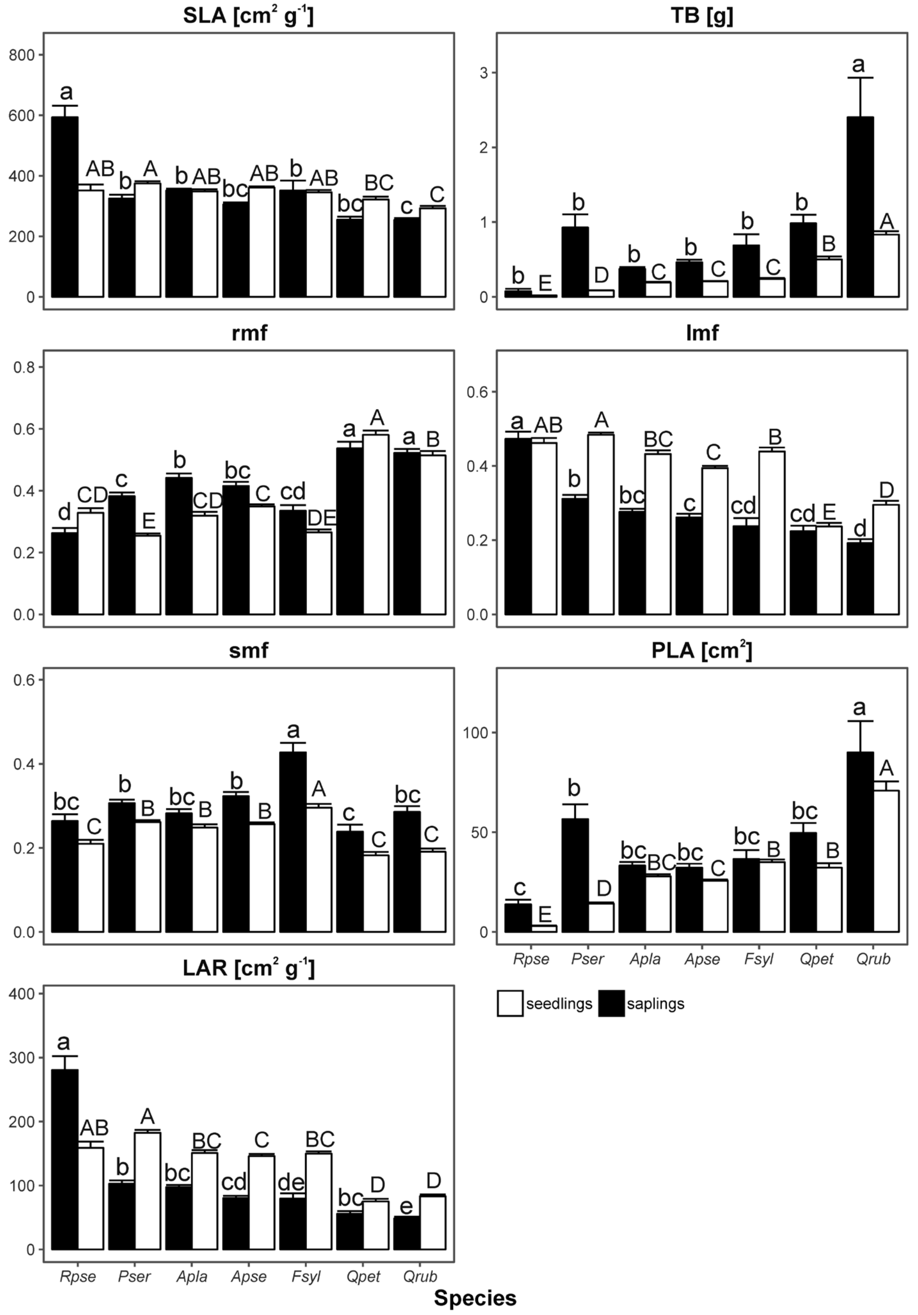

Figure 2. Mean (+SE) values of species traits of natural regeneration: SLA – specific leaf area (cm^2 g^{-1}), TB – total biomass [g], rmf – root mass fraction, lmf – leaf mass fraction, smf – stem mass fraction, PLA – projected leaf area [cm^2], LAR – leaf area ratio [cm^2 g^{-1}]. Differences were assessed using one-way mixed effects ANOVA and Tukey *post hoc* tests – species marked by the same letter (lower-case letters for saplings and upper-case letters for seedlings) did not differ significantly statistically ($p<0.05$). ANOVA details are provided in Suppl. material 1: Table S1. Species are ordered according to successional stages.

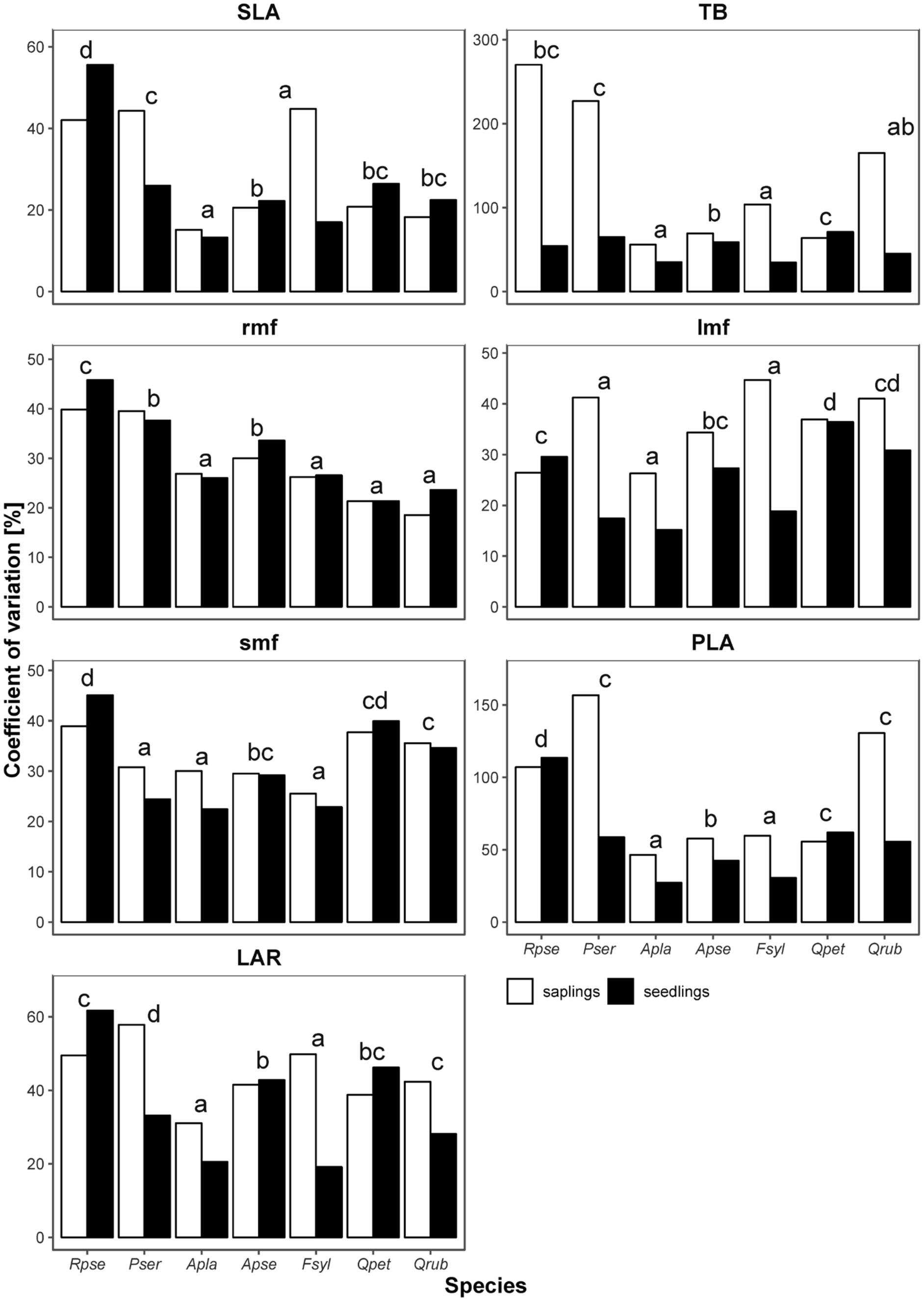

Figure 3. Coefficients of variation for age stages and parameters: SLA – specific leaf area (cm^2 g^{-1}), TB – total biomass [g], rmf – root mass fraction, lmf – leaf mass fraction, smf – stem mass fraction, PLA – projected leaf area [cm^2], LAR – leaf area ratio [cm^2 g^{-1}]. The same letters species which did not differ statistically significantly ($p>0.05$) in pairwise comparisons by modified signed-likelihood ratio (M-SLR) tests of differences. Tests revealed the same division into species groups for both saplings and seedlings.

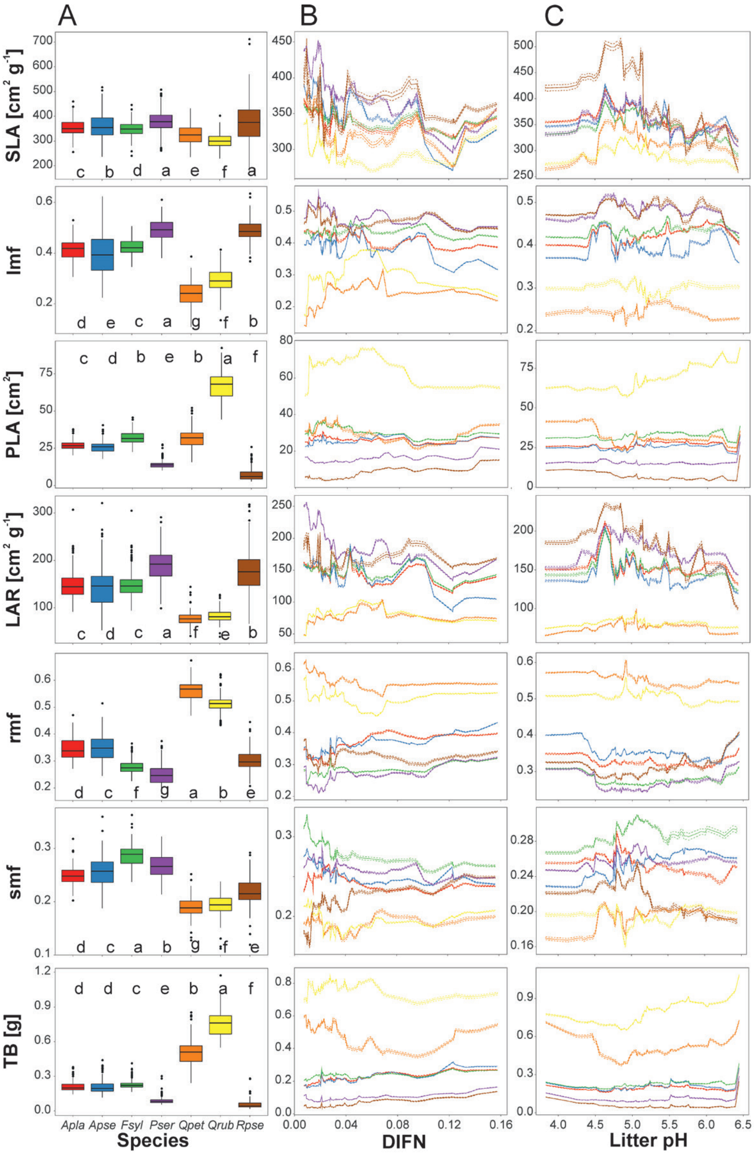

Figure 4. Saplings traits variability of the species studied across predictors explained by a random forest model. Partial dependence plots (ceteris paribus plots) show changes of predicted values when a particular predictor is changed while all remaining predictors are constant (i.e. mean value) – in the middle (**B**) and right (**C**) column we showed interactions between species and DIFN and litter pH. In the left column (**A**) we showed partial group predictions – predicted trait values assuming constant levels of other predictors, boxes represent interquartile range and median, whiskers represent minimum-maximum range, abbreviations of species: *Apla – Acer platanoides*, *Apse – A. pseudoplatanus*, *Fsyl – Fagus sylvatica*, *Pser – Prunus serotina*, *Qpet – Quercus petraea*, *Qrub – Q. rubra*, *Rpse – Robinia pseudoacacia*; traits: SLA – specific leaf area, lmf – leaf mass fraction, PLA – projected leaf area, LAR – leaf area ratio, rmf – root mass fraction, smf – stem mass fraction, TB – total biomass. For further details see Table 1. Species marked by the same letter did not exhibit significant statistical difference in predicted trait values, according to the Tukey posteriori test at p=0.05.

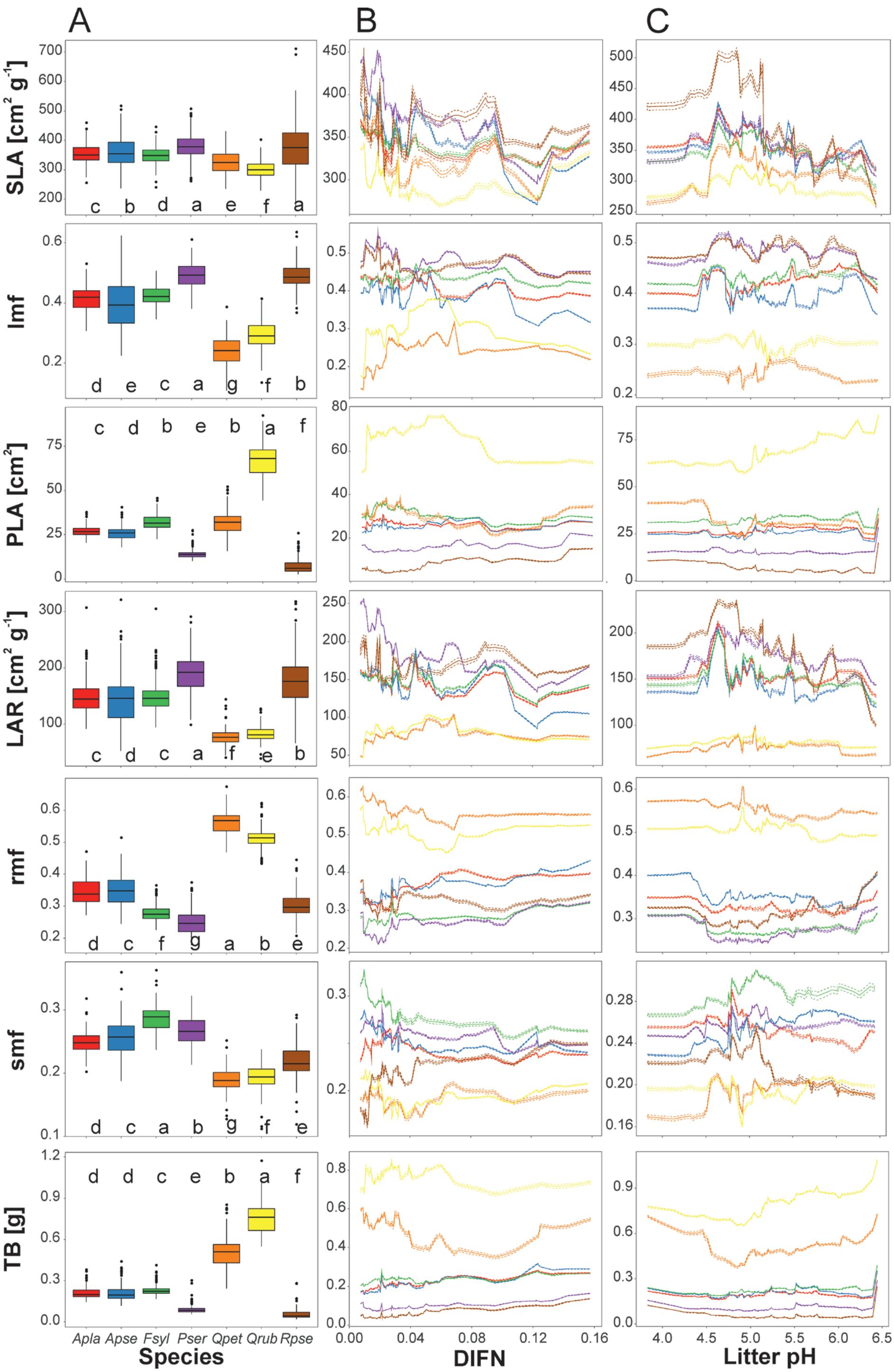

Figure 5. Seedlings traits variability of the species studied across predictors explained by a random forest model. For explanations see Fig. 4.

Table 1. Parameters of random forest models for traits and age classes and predictors importance expressed by drop-out loss of RMSE. Abbreviations: SLA – specific leaf area, lmf – leaf mass fraction, PLA – projected leaf area, LAR – leaf area ratio, rmf – root mass fraction, smf – stem mass fraction, TB – total biomass. Bold value indicate predictor with the highest importance.

Age	Trait	Unit	R^2	RMSE	Drop-out loss of RMSE – pH	Drop-out loss of RMSE – DIFN	Drop-out loss of RMSE – species
saplings	SLA	$cm^2\ g^{-1}$	0.585	95.040	106.517	94.999	**181.012**
	Lmf	–	0.431	0.095	0.104	0.094	**0.121**
	PLA	cm^2	0.212	60.257	60.768	61.505	**66.031**
	LAR	$cm^2\ g^{-1}$	0.696	46.944	50.947	53.637	**85.165**
	Rmf	–	0.405	0.113	0.108	0.126	**0.131**
	Smf	–	0.147	0.095	0.088	0.094	**0.096**
	TB	g	0.279	1.603	1.618	1.893	**1.912**
seedlings	SLA	$cm^2\ g^{-1}$	0.129	99.242	**92.906**	89.672	90.265
	Lmf	–	0.436	0.094	0.091	0.102	**0.146**
	PLA	cm^2	0.552	14.887	15.474	15.687	**27.284**
	LAR	$cm^2\ g^{-1}$	0.408	53.011	55.492	55.876	**71.275**
	Rmf	–	0.468	0.109	0.105	0.111	**0.172**
	Smf	–	0.178	0.072	0.073	0.074	**0.084**
	TB	g	0.662	0.161	0.160	0.163	**0.329**

Discussion

Trait values

Our study revealed that alien and native species differed the most in SLA, rmf, lmf and LAR; however the variability was usually not related to the resource gradients. This is connected with high inter-specific variability of functional traits, which results from different morphology and phylogeny of species studied (e.g. Poorter et al. 2015). For example, analysis of seasonal variability of 12 herbaceous species SLA, biomass and TLA(i.e. along DIFN temporal gradient) growing in the same locality also revealed a higher range of interspecific differences than during ontogeny within species (Jagodziński et al. 2016). For that reason previous studies focused on phylogenetically-related pairs of species (e.g. Grotkopp et al. 2010), to reduce phylogenetic structures from analyses (Roberts et al. 2017). However, in natural conditions species are co-occurring regardless of phylogenetic relativity. Thus, the success of some invasive species is claimed to be connected to being different from native species in terms of functional traits, e.g. by colonizing empty niches or by ability to break habitat filtering (Melbourne et al. 2007; Hierro et al. 2005).

The differences among species reflect higher investment in leaves and a more acquisitive strategy of alien species, especially in the cases of *P. serotina* and *R. pseudoacacia*. These species used higher investment in foliage and higher SLA as ways of increasing PLA. SLA is a strongly acquisitive trait, correlated with photosynthetic capacity (Wright et al. 2004), as well as with ruderal and competitive life strategies (Westoby 1998). *Q. rubra* did not differ in these traits from native species but revealed higher biomass allocation to root systems. This is in line with previous observations indicating higher root:shoot ratio of *Q. rubra* (Kuehne et al. 2014). The investment in leaves and roots is a predictor of total biomass (Enquist and Niklas 2002; Poorter et al. 2015) – the higher these parameters are, the lower the total biomass. However, this assessment covered the whole spectrum of plants. At the stage of saplings higher investment in leaves resulted in higher total leaf area and competitive advantage over native species in limited light availability (te Beest et al. 2015). Nevertheless, previous studies are equivocal in assessing differences in lmf and rmf between alien and native species. Some of these studies indicated a lack of differences in rmf (Grotkopp et al. 2010; Matzek 2011) while some showed higher rmf (Kuehne et al. 2014) and some lower rmf (Paquette et al. 2012; González-Muñoz et al. 2014) of alien species. Biomass allocation to the root systems also depends on root competition (Kawaletz et al. 2014). Investment in acquisitive traits causes a competitive advantage over native species (Blossey and Notzold 1995; te Beest et al. 2015).

Our study revealed differences between seedlings and saplings in case of most traits and species. These differences are mostly connected with different leaves morphology (Cierjacks et al., 2013; Annighöfer et al., 2016). The youngest leaves are usually thinner than older ones, which results in higher SLA and PLA. This may influence low survival of seedlings (Beckage and Clark 2003; Canham and Murphy 2016; Knight et al. 2008). For TB and PLA, seedlings of alien species had lower values than native species, while saplings had higher values. This may show that alien species do not have a biomass advantage in the first year of life. This comparison of alien and native species is biased by the outstandingly high biomass of *Q. rubra*. However, this species also differs from the other alien species studied in leaf-root allocation. This may indicate that the alien species studied had two ways to achieve the same goal – high leaf area. In the case of smaller plants the goal was realized by changes in biomass allocation and in the case of *Q. rubra* – by high biomass. Similar differentiation of alien species into acquisitive and conservative was found by Tecco et al. (2013). Higher biomass production and PLA was also mentioned as a factor connected with invasiveness (Grotkopp et al. 2010; Kuehne et al. 2014; Jo et al. 2015).

Trait variability

Our results revealed that *P. serotina* and *R. pseudoacacia* mostly had higher CV than native species. However, this was not always connected with higher variability of alien species traits along resources availability gradients, which may indicate high variability of trait values within young generations of invasive species. Most previous studies revealed differences in phenotypic plasticity between alien and native species (Paquette et al. 2012; Lamarque et al. 2013; Hou et al. 2014). Kuehne et al. (2014) did not find differences in phenotypic plasticity of *Q. rubra* and three co-occurring native species. Our study indicated that for acquisitive traits, variability of *Q. rubra* traits, expressed by interaction with environmental gradients, also did not differ from native species.

Assuming high propagule pressure, observed high variation in trait values may be the reason for their ecological success. However, most of the previous studies found that this variability was connected to phenotypic plasticity (e.g. Davidson et al. 2011;

Paquette et al. 2012; Lamarque et al. 2013). Nevertheless, in our study we cannot distinguish which part of variability is driven by phenotypic plasticity, due to lack of data about each individual provenance. Neutral theory assumes similar probability of mortality, speciation and reproduction within the same functional guild (Hubbell 2001). Application of this theory to invasion ecology highlights the need of accounting for the randomness in modeling community structure and functioning (Daleo et al. 2009). This randomness may be reflected in high variation of traits and high density of alien species seedlings and saplings, which allow for survival of the best fit individuals. This interpretation is strongly in line with previous studies highlighting the role of propagule pressure in ecological success of invasive species (Lockwood et al. 2005; Vanhellemont et al. 2009; Pyšek et al. 2015; Dyderski and Jagodziński 2018a). This speculation may be solved by testing whether survival of alien species seedlings depends on resource availability per plot, or shows a random pattern.

Trait responses to resource gradients

Our study revealed that alien species had a more acquisitive strategy of light acquisition, expressed by higher LAR than native species. The effects of resource availability on the leaf traits studied – lmf, LAR and SLA – were lower than differences between alien and native species. Also Robakowski et al. (2018) found high importance of light availability on lmf, rmf and photosynthesis efficiency in *P. serotina* and *Q. petraea*. Previous studies usually considered the effects of resource availability on particular species (Funk 2008; Lamarque et al. 2013; Kuehne et al. 2014) or phylogenetically related pairs of alien and native species (Allison and Vitousek 2004; Grotkopp et al. 2010; Matzek 2011). Only a few studies accounted for ecologically related alien and native species – i.e. co-occurring in one ecosystem type (González-Muñoz et al. 2014; Kuehne et al. 2014; te Beest et al. 2015). This lack of real relationship was raised as an important concern by Hulme (2008). Moreover in our study alien species occur and regenerate spontaneously in the study plot system.

Comparing litter pH and light availability gradients, differences between alien and native species traits were usually clearer along the DIFN gradient. The exception was PLA and (for saplings only), SLA and TB. We would expect that SLA will differ mostly due to light availability, as this factor drives SLA variability (Jagodziński et al. 2016). However, as SLA is nitrogen-dependent (Wright et al. 2004; Díaz et al. 2016), this trait also differed with litter pH, which is a proxy for general soil fertility and nitrogen content. For that reason SLA increases with litter pH and decreases with DIFN (Table 1). In the cases of lmf and LAR effect sizes of pH were lower. This indicates that general investment in foliage – both based on higher allocation and on leaf morphology (SLA) – is a reaction to light availability. Thus, as invasive species studied strongly modify environment, especially light availability and litter chemistry (e.g. Allison and Vitousek 2004; Knight et al. 2008; Horodecki and Jagodziński 2017), traits of natural regeneration might be influenced by invasive species presence in overstory. This feedback may be more important in case of alien species studied, as their abundance is strongly related to the presence of parental trees (Dyderski and Jagodziński 2018a). However, native species are also able to strongly decrease light availability (e.g. *Acer* spp., *Fagus sylvatica*) or rate of nutrients cycling by low decomposition rate of leaf litter (Dobrylovská 2001; Horodecki and Jagodziński 2017). Thus, in our study we investigated effect of resources availability rather than alien-native species-specific effects of overstory.

Consequences for ecological success of invasive species

Invasive species studied revealed three different patterns of biomass investment differentiating them from the native species. *R. pseudoacacia* realized strategy 'try hard' in terms of investment in foliage, supporting the suggestion of Tecco et al. (2010) that invasive species invest more in acquisitive traits. In contrast, *Q. rubra* represents rather conservative strategy (Tecco et al. 2013) – invests in traits connected with persistence – low SLA, and in belowground resources competition. However, this strategy seems to be effective, as this species reaches higher individual biomass and high projected leaf area. Although *P. serotina* has higher lmf, its SLA and LAR places this species among native ones. This would suggest that *P. serotina* rather 'joins the locals' – represents similar life strategy to its most frequent competitors. All of these strategies lead to high total leaf area, which allows for out-shading native vegetation and reducing competitors (te Beest et al. 2015). The three species studied are the most frequent alien woody species in European forests (Wagner et al. 2017). Therefore, we conclude that both strategies are effective ways to reach ecological success, in contrast to Tecco et al. (2010; 2013), who claimed that an acquisitive strategy is more efficient. However, we found very limited support for variability of traits across interactions of species and resource gradients. Despite high variability and differences among species, this suggest that invasive species success is not related to the species traits variability. Thus, all three species are rather limited by propagule pressure, which is the main factor driving their biomass in the plant communities studied (Dyderski and Jagodziński 2018a). High variability of invasive species traits also suggests randomness in seedling survival, which similarly to neutral theory of invasion, highlights the necessity of including randomness in modelling biological invasions.

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Supplementary material 1

Supplementary materials

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Data type: statistical data

Explanation note: **Table S1.** Mixed-effects ANOVA models of traits studied (LAR – leaf area ratio [cm^2 g^{-1}], lmf – leaf mass fraction, PLA – projected leaf area [cm^2], rmf – root mass fraction, SLA – specific leaf area (cm^2 g^{-1}), smf – stem mass fraction, TB – total biomass [g]) and across species studied. R^2m is the amount of variance explained by fixed effects only and R^2c – by both fixed and random effects.; **Table S2.** Differences between seedlings and saplings in traits studied (LAR – leaf area ratio [cm^2 g^{-1}], lmf – leaf mass fraction, PLA – projected leaf area [cm^2], rmf – root mass fraction, SLA – specific leaf area (cm^2 g^{-1}), smf – stem mass fraction, TB – total biomass [g]) within species studied assessed using t-tests.; **Figure S1.** Species Co-occurrence matrix for seedlings and saplings of the species studied. Co-occurrence was calculated using co-occur R package (https://cran.r-project.org/web/packages/cooccur/index.html), based on presence-absence of species studied with 372 study plots in 2015. The type of co-occurrence (positive, negative and random) between species pairs was assessed basing on observed and expected occurrence probabilities.

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