

Research Article

Invasive *Prunus serotina* vs. *Robinia pseudoacacia*: How does temperate forest natural regeneration respond to their quantity?

Sebastian Bury¹ , Marcin K. Dyderski¹ 

¹ Institute of Dendrology, Polish Academy of Sciences, Parkowa 5, 62-035 Kórnik, Poland

Corresponding author: Sebastian Bury (sbury@man.poznan.pl)

Abstract

Invasive trees negatively impact forests, by making the vegetation more homogeneous when invaders are present than when they are absent. Here, we aim to more deeply understand the effects of invasive trees on forests with a focus on seedlings and saplings and how they respond to continuous variation in aboveground biomass of invaders rather than presence/absence. Our findings are useful for close-to-nature silviculture, as they elucidate how much natural regeneration will change under particular biomasses of invasive species. Specifically, we evaluate the relationships of two invasive tree species: black cherry *Prunus serotina* Ehrh. and black locust *Robinia pseudoacacia* L. with natural tree regeneration in temperate forests. We established 160 circular 0.05 ha plots in western Poland managed forests, in two different habitat types: nutrient-poor with *Pinus sylvestris* L. and nutrient-rich with *Quercus* spp. We assessed natural regeneration by counting all trees < 1.3 m in height, within four circular subplots ($r = 3$ m). Relationships between invader biomass and regeneration of other tree species were idiosyncratic. Natural regeneration of dominant forest-forming tree species (*P. sylvestris*, *Quercus petraea*) decreased with increasing invader biomass, while shade-tolerant, nitrophilous tree and shrub regeneration increased with invader biomass. The most negatively correlated were *P. sylvestris* in nutrient-poor habitats and *Q. petraea* in both nutrient-poor and rich habitats. We observed increased density of other non-native species as *R. pseudoacacia* abundance increased, in line with the invasional meltdown hypothesis.

Key words: Advance regeneration, black cherry, black locust, invader aboveground biomass, invasion ecology, *per capita* effect, saplings, seedlings



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Sebastian Bury & Marcin K. Dyderski.

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Introduction

Regeneration is a crucial element of forest stability and continuity (Oliver and Larson 1996; Baraloto et al. 2005; Käber et al. 2023). This process occurs through planting or sowing — artificial regeneration, or naturally without human impact — natural regeneration (Jaworski et al. 2007; Nyland 2007). Natural regeneration is essential in natural forests, without human impact, but also plays an increasing role in managed forests. Using natural regeneration of forests is part of what is called close-to-nature, ecological forestry (Batavia and Nelson 2016; Palik and D’Amato 2017). Closer to nature forestry is based to a greater extent on the natural dynamics of tree stands, which results in an increase in the complexity of their structure and increased biodiversity (European Commission 2023). Naturally regenerated stands are characterized by higher genetic diversity than forest

plantations. Such stands are therefore characterized by greater resistance and greater adaptation to local environmental conditions (Jaworski et al. 2007; European Commission 2023). Additionally, natural regeneration is more cost-effective than artificial regeneration (Oluwajuwon et al. 2024).

The natural regeneration of forests is shaped by abiotic and biotic factors. Abiotic factors include climate (Canham and Murphy 2017), light availability (Minotta and Pinzauti 1996; Modrý et al. 2004), and soil characteristics (Minotta and Pinzauti 1996; Madsen and Larsen 1997; Modrý et al. 2004). Biotic factors include diseases (e.g., Bakys et al. 2009; Lygis et al. 2014; Turczański et al. 2021), herbivory (Ammer 1996; Bruinderink and Hazebroek 1996; Iszkuło et al. 2013; Borkowski et al. 2017; Szwagrzyk et al. 2020) and competition with other plants (Mölder et al. 2019; deGroot et al. 2022; Li et al. 2023). Disturbances, including fire (Il'ichev et al. 2011) and windthrows (Szwagrzyk et al. 2018) can create gaps in the forest that alter both the abiotic and biotic environment and provide good conditions for the growth of young trees. Additionally, natural regeneration relies on seed availability (Howe and Smallwood 1982; Bartlow et al. 2018; Czortek et al. 2024). Finally, natural regeneration processes are influenced by human activities related to forest management, e.g., timber harvesting (Tavankar et al. 2017; Picchio et al. 2020), post-disturbance management (Marcolin et al. 2019), and climate change (Boucher et al. 2020; Enríquez-de-Salamanca 2022). Thus, natural regeneration depends on many factors, abiotic and biotic, natural and influenced by humans. Many of these factors that influence forest regeneration can be further shaped by invasive species, which alter both the abiotic and biotic environment.

Invasive trees and shrubs are well known for their ability to transform the recipient ecosystem (e.g., Crooks 2002; Corenblit et al. 2014; Jagodziński et al. 2024), e.g., by changes in nutrient cycling and decomposition (Aerts et al. 2017; Horodecki et al. 2019) or light availability (Starfinger et al. 2003; Dyderski and Jagodziński 2019; García et al. 2023). Those transformations can also impact the understory, including saplings and seedlings (Fuentes-Ramírez et al. 2011; Terwei et al. 2013; Dyderski and Jagodziński 2020; Langmaier and Lapin 2020). A review of studies assessing the impact of invasive plants on natural regeneration (Langmaier and Lapin 2020) identified 74 studies in Europe. Most of these studies evaluate natural regeneration based on cover and have revealed important impacts of invasive species (e.g., Maskell et al. 2006; Hejda 2012; Petrášová et al. 2013; Tinya et al. 2019). Cover, though important, does not provide reliable estimates of population size, and thus additional research on the impacts of forest invaders using precise counts of seedlings and saplings will aid in projecting forest health into the future (Terwei et al. 2013). Additionally, most studies on forest invasion compared invaded stands with uninvaded ones (Gentili et al. 2019; Lanta et al. 2022; Slabejová et al. 2023). While this is an important first step, understanding the effects of invader abundance, i.e. the *per capita* effects of invasive plants will provide more actionable information for forest management. This has only rarely been done for either herbaceous plants (Czortek et al. 2023; Wiatrowska et al. 2023) or invasive woody plants (Chabrierie et al. 2008; López-Núñez et al. 2017; García et al. 2023; Bury and Dyderski 2024b, 2024a; Jagodziński et al. 2024) with a focus on biodiversity or ecosystems services. However, to our knowledge, there are no studies assessing the effects of invader abundance on native species natural regeneration.

To address these knowledge gaps, we investigated the relationship between forest natural regeneration and the abundance of two invasive tree species, *Prunus serotina*

and *Robinia pseudoacacia*. To capture various environmental contexts, we focused on two forest types dominated by either *Pinus sylvestris* or *Quercus* spp.

Prunus serotina and *Robinia pseudoacacia* differ in their biology and ecology. Both are native to North America and were introduced to Europe in the 17th century as ornamental trees. In the following centuries, they were planted by foresters as soil-improving and wood-production trees (Starfinger et al. 2003; Cierjacks et al. 2013). Currently, *P. serotina* (Starfinger et al. 2003) and *R. pseudoacacia* (Sádlo et al. 2017; Vítková et al. 2017; Slabejová et al. 2023) are common invasive trees in Central Europe. *Prunus serotina* is mostly a shrub or small tree found in gaps (Godefroid et al. 2005; Closset-Kopp et al. 2007, 2011). It is mostly dispersed by mammals (Kurek et al. 2024), birds, or gravity (Starfinger et al. 2003; Deckers et al. 2008). *Prunus serotina* increases the soil nutrient pool, compared to native tree species, due to the higher leaf nutrient content and decomposition rate (Aerts et al. 2017; Horodecki et al. 2019). *Robinia pseudoacacia* is a pioneer tree associated with big, open patches that attains large size and occurs in the highest forest strata (Cierjacks et al. 2013; Bury and Dyderski 2024b), associated with big, open patches. Seeds of *R. pseudoacacia* are dispersed by wind and gravity (Vítková et al. 2017), though much of its spread is vegetative (Bouteiller et al. 2023). As a tree in the Fabaceae, *R. pseudoacacia* creates symbiosis with nitrifying bacteria (Rice et al. 2004; Vítková et al. 2017) and thus delivers a large amount of nitrogen to the soil largely through leaf litter (Rahmonov 2009).

We address five hypotheses in our work. (H1) We hypothesized that patterns of forest regeneration will differ in association with the two invaders. We assume that *R. pseudoacacia* and *P. serotina* will shape interactions among species and their environment in different ways, which will be manifested by different patterns of natural regeneration densities (Dyderski and Jagodziński 2020; Langmaier and Lapin 2020). (H2) We expected the regeneration of trees and shrubs to vary with invader abundance in species-specific ways (Terwei et al. 2013; Dyderski and Jagodziński 2018). (H3) Likewise, we hypothesized that there would be differences between nutrient-rich and nutrient-poor sites (Chmura 2004; Halarewicz 2011). (H4) We hypothesized that other non-native tree species may have higher regeneration densities in the presence of studied invaders, according to the invasional meltdown hypothesis (Simberloff and Holle 1999). Finally, we aimed to compare patterns obtained using three different statistical approaches (ordination, Threshold Indicator Taxa Analysis, and generalized linear mixed-effects models) to provide insights into which is best suited to the type of data we collected. (H5) We hypothesized that these three methods would provide consistent results regarding the effects of studied invaders on particular tree species' natural regeneration.

Methods

Study area and study design

We conducted the study in managed forests in western Poland, in five forest districts: Babki, Czarniejewo, Jarocin, Konstantynowo, and Łopuchówko (Fig. 2). We located study plots between 51°59'4.08"N and 52°40'9.36"N and 16°35'28.98"E and 17°37'13.26"E, in two geographical regions: the Greater Poland Lakeland (northern part) and Greater Poland Lowland (southern part). The climatic conditions are similar in the study area with an annual temperature of 8.5 °C and mean annual precipitation of 500–550 mm (BDL 2024).

We aimed to sample a quantitative gradient of invader biomass. To obtain a range, we selected study plots based on invader cover, which is straightforward to estimate, and then, after plots were chosen, we quantified aboveground biomass, following established methods (Bury and Dyderski 2024b), and described in more detail below. During initial plot selection we search for control plots (zero individuals of studied invaders ≥ 1.3 m height), medium ($< 30\%$ cover), and high ($> 50\%$) cover areas. Therefore, in our plots there could have been *P. serotina* or *R. pseudoacacia* individuals shorter than 1.3 m (included in the natural regeneration survey), however, they were rare as the density of studied neophytes depends on the proximity of propagule sources (Dyderski and Jagodziński 2018). When calculating the gradient of invader biomass, we accounted only for individuals taller than 1.3 m, and the biomass of those few individuals in the regeneration layer in control plots was negligible. We stratified our samples into two habitat types: nutrient-rich habitats that are typical of the invasive species in their native range, and nutrient-poor, where invaders had been massively introduced to improve these habitats (Starfinger et al. 2003; Cierjacks et al. 2013). Nutrient-poor sites included *Leucobryo-Pinetum* W. Mat. (1962) 1973 communities or secondary *P. sylvestris* forests. In our study, nutrient-rich sites include different subtypes of *Galio sylvatici-Carpinetum betuli* Oberd. 1957 communities or secondary *Quercus* spp. forests. Some areas had characteristics of poorer communities or slightly more fertile ones, with species characteristic of *Potentillo albae-Quercetum* Libb. 1933 or *Quercu-roboris Pinetum* Mat. et Polak. 1955 s.l. We also included two management contexts: stands in the middle of rotation age (medium age) and close to rotation age (mature age), as these age classes differ in light conditions beneath stand canopies. Stands in the middle age and those of close to rotation age differ in structure and growth dynamics (Jiang et al. 2017; Li et al. 2024). Middle-aged stands are characterized by a rapid increase in biomass, while stands close to rotation age are characterized by maximum biomass, but its increment decreases with age (Jiang et al. 2017; Li et al. 2024). Stand age is related to light availability by stem density and canopy closure, as well as in terms of higher species richness of forest specialists, related to a longer time since disturbance (Jagodziński and Oleksyn 2009; Felton et al. 2010; Conradi et al. 2020). In total, we established 160 plots (500 m² per plot), including 32 control plots (8 replications \times 2 habitat types \times 2 stand age classes), 64 plots with *R. pseudoacacia* (8 replications \times 2 invasion levels \times 2 habitat types \times 2 stand age classes) and 64 plots with *P. serotina* (same as *R. pseudoacacia*) (Fig. 1). Plots representing the same plot variant (invader \times invasion level \times habitat \times stand age) were a minimum of 5 km apart to reduce spatial autocorrelation.

Invasive species quantitative gradient – aboveground biomass

We estimated invader biomass of 102 plots in the autumn of 2021 and 2022, measuring the diameter at breast height (DBH) of all the individuals in the plots following García et al. (2023). The other 58 plots were sampled in autumn 2022 and 2023. For these, we measured the diameter at the breast height only on trees larger than 5 cm, and we counted trees thinner than 5 cm by species. Then, from the database of the 102 plots, we calculated the average DBH of individuals thinner than 5 cm by species (Suppl. material 1: table S1 for mean and SD values). This approach should not affect the validity of the



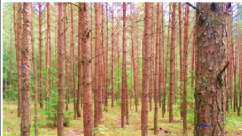
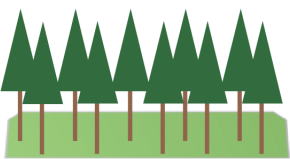



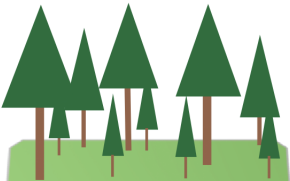


| | INVADER | INVASION LEVEL | HABITAT | STAND AGE |
|----------------|---|---|---|--|
| 8 REPLICATIONS | <i>P. serotina</i>  | Medium (<30%)  |  <u>Low</u> (nutrient-poor habitats with Scots pines) |  <u>Medium</u> (40-80 years old) |
| | <i>R. pseudoacacia</i>  | High (>50%)  |  |  <u>Mature</u> (Scots pine: 80-120 years old; Oaks: 100-140 years old) |
| | <u>Control</u>  | <u>Control</u> (0%)  | <u>High</u> (nutrient-rich habitats with oaks) | |

Figure 1. Scheme of the study design. Photos: S. Bury.

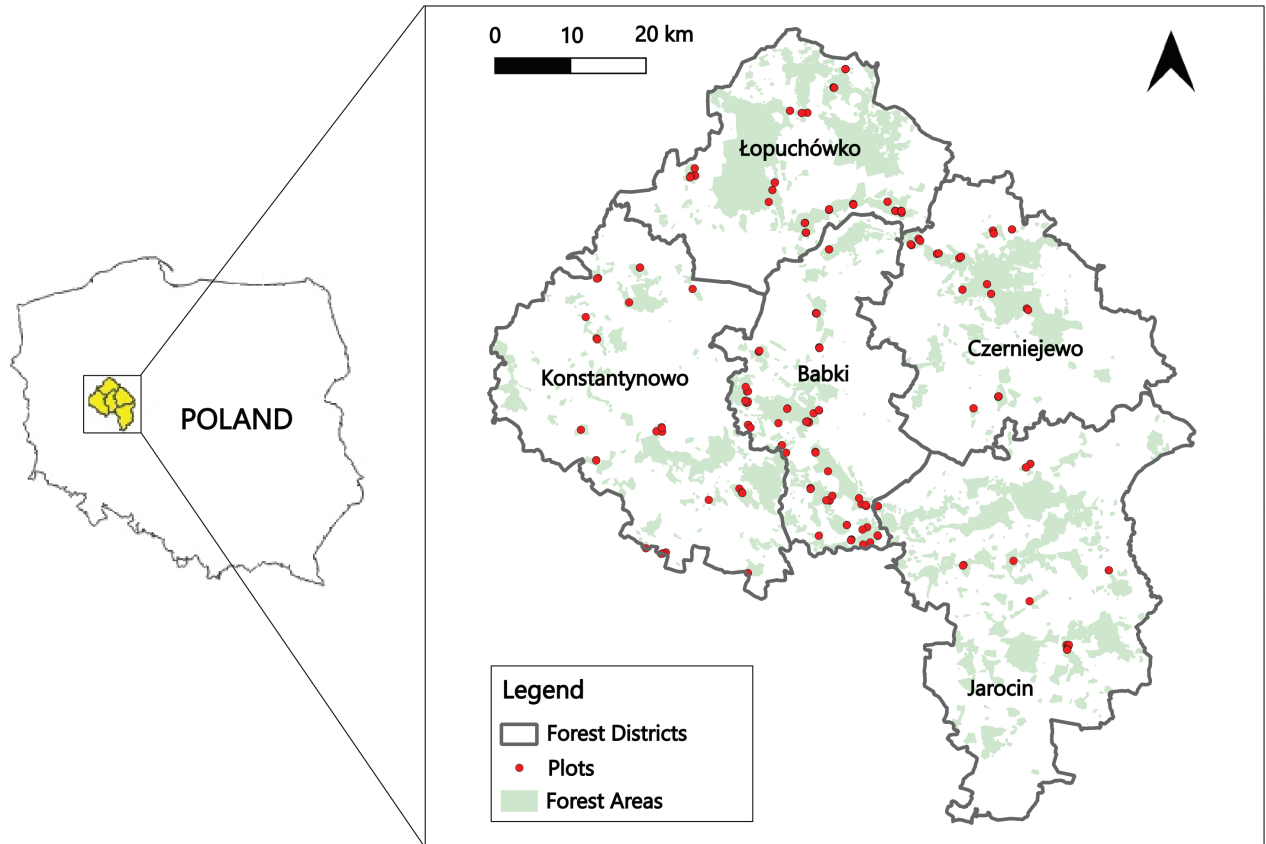


Figure 2. Distribution of the study plots (n = 160). The background map of forest cover comes from the Forest Data Bank (BDL 2024).

results, and indeed is more detailed than previous studies that either omitted trees with $DBH < 5$ cm or used a DBH midpoint for smaller trees (Dyderski and Jagodziński 2021a). Then, we used published allometric formulas (Suppl. material 1: tables S2–S3) to calculate the aboveground biomass for individual trees and stands (Brown 1976; Alberti et al. 2005; Forrester et al. 2017; Zasada 2017; Jagodziński et al. 2018, 2019).

Assessment of natural regeneration

In the summers of 2021, 2022, and 2023 we counted natural regeneration on four schematically distributed subplots with a 3 m radius ($4 \times 28.26 \text{ m}^2 = 113.04 \text{ m}^2$). The centers of the subplots were systematically set at 4.21 m (1/3 of the main plot radius) from the center of the plots in the four cardinal directions (N, E, S, W), using a compass and measuring tape (Fig. 3). Within these subplots we identified and counted all individuals of trees and shrubs < 1.3 m height, similarly to Kerr and Mackintosh (2012) and Mousavi et al. (2012). For each plot, we identified all seedlings germinated in the study year by species, as well as all saplings up to 1.3 m in height. Saplings may have been the product of prior years' seedlings, or clonal propagation. We treated all saplings growing separately from the soil as single individuals (Radtke et al. 2013).

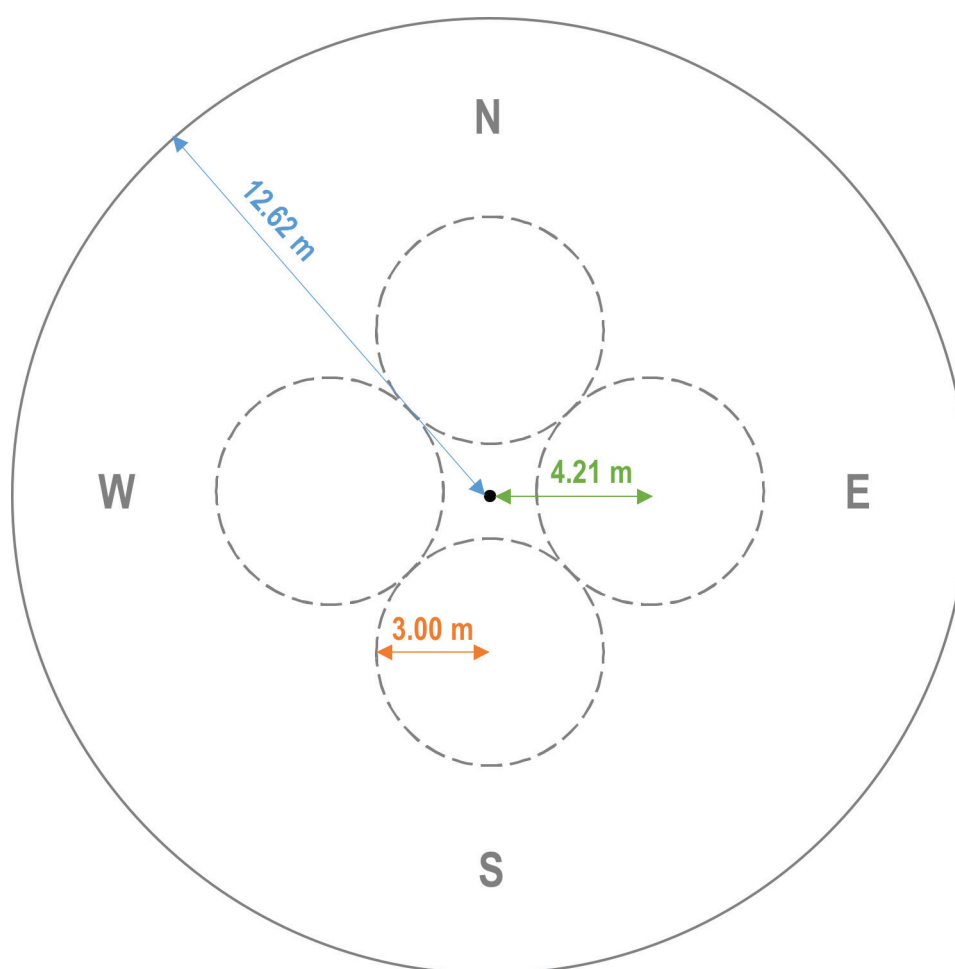


Figure 3. Schematic of the distribution of the subplots (four dashed line circles, counts of natural regeneration) within each plot (solid line circle, stand structure measurements). Plot area = 500 m^2 ($r = 12.62 \text{ m}$), subplots area = $4 \text{ subplots} \times 28.26 \text{ m}^2 = 113.04 \text{ m}^2$ ($r = 3 \text{ m}$).

Data analyses

All analyses were conducted in R (R Core Team 2023). Because one of the plots with *P. serotina* in the stand (*P. serotina* aboveground biomass = 47.11 Mg ha⁻¹; Table 1) gave a strongly biased result, we excluded it from all analyses. The aboveground biomass of *P. serotina* trees in this area was about three times higher than the next highest result. Due to differences in species pools in each habitat type, we separately analyzed the relationships with the natural regeneration for both studied invaders on both habitats. We accounted for different stand development phases, including stand age as a covariate in analyses.

We used Canonical Correspondence Analysis (CCA) to compare the effect of invader biomass and stand age. We used the `cca()` function from the `vegan` package (Oksanen et al. 2018) to develop CCA. Due to differences in sapling density among species and plots, we log-transformed data using the `decostand()` function from the `vegan` package (Oksanen et al. 2018). Furthermore, we added invader aboveground biomass and stand age as constraints. We used the `step.cca()` function from the `vegan` package to choose the optimal set of predictors based on Akaike’s Information Criterion. To assess the significance of constraints, we ran a permutation-based ANOVA-like test, implemented in the `anova.cca()` function. We visualized the results using the `ggplot2` (Wickham 2016) and `ggrepel` (Slowikowski 2024) packages.

Furthermore, we used Threshold Indicator Taxa Analysis, implemented in the TITAN2 package (Baker et al. 2023) to check which sapling species increase or decrease with invader biomass. We log-transformed biomass using $\log(x+1)$ transformation, to include also plots with zero invader biomass. For species with purity and reliability ≥ 0.95 we visualized results using the `plot_taxa_ridges()` function with default settings. We conducted the analysis using only species that occurred in at least three plots. We did not use any additional filters in the settings. The `plot_taxa_ridges()` function generates graphs on which the x-axis represents an environmental factor. In our case, this is the aboveground biomass of an invasive species ($\log(x+1)$ transformation was used). Changes in the abundance of individual taxa were assessed along the gradient of the environmental variable. In our case, this was the number of saplings of individual species on the plot. Ridges are generated for species that have achieved purity and reliability of 95%. These ridges look different for each species. The shape of the ridge tells us where in the environmental gradient a given species achieves the highest probability of occurrence.

Table 1. General characteristics of the studied plots: stand age, total aboveground biomass, invasive tree species aboveground biomass. *Quercus* — nutrient-rich habitats with *Q. petraea/robur*, *Pinus* — nutrient-poor habitats with *P. sylvestris*.

| | Stand age [years] | | | | Total Aboveground Biomass [Mg ha ⁻¹] | | | | Invader Aboveground Biomass [Mg ha ⁻¹] | | | |
|-----------------------------|-------------------|-------|-------|------|--|--------|--------|--------|--|-------|-------|--------|
| | Min. | Mean | SD | Max. | Min. | Mean | SD | Max. | Min. | Mean | SD | Max. |
| Control | | | | | | | | | | | | |
| <i>Quercus</i> | 47 | 93.75 | 33.28 | 139 | 157.38 | 278.74 | 100.16 | 507.92 | 0.00 | 0.00 | 0.00 | 0.00 |
| <i>Pinus</i> | 50 | 76.00 | 22.82 | 117 | 142.95 | 187.17 | 34.50 | 254.63 | 0.00 | 0.00 | 0.00 | 0.00 |
| <i>Prunus serotina</i> | | | | | | | | | | | | |
| <i>Quercus</i> | 44 | 90.31 | 31.96 | 137 | 138.12 | 267.52 | 93.24 | 505.01 | 0.19 | 6.68 | 7.24 | 27.39 |
| <i>Pinus</i> | 45 | 71.59 | 21.78 | 108 | 142.37 | 196.99 | 33.25 | 256.66 | 0.18 | 7.34 | 8.75 | 47.11 |
| <i>Robinia pseudoacacia</i> | | | | | | | | | | | | |
| <i>Quercus</i> | 42 | 94.56 | 34.24 | 139 | 147.63 | 317.01 | 141.48 | 709.91 | 0.82 | 50.77 | 70.37 | 278.24 |
| <i>Pinus</i> | 42 | 76.81 | 23.06 | 117 | 125.32 | 182.14 | 31.44 | 246.52 | 0.22 | 20.91 | 31.69 | 153.00 |

The top of the ridge indicates the value of the environmental indicator for which the abundance of the species is the highest. The greater the width of the ridge, the greater the discrepancies in the data. Taxa are divided into two groups. Species whose abundance increases along the environmental gradient are marked in red (increasers), while species whose abundance decreases along the environmental gradient are marked in gray/blue (they are called decliners). The z-score value indicates the strength of the impact of a given factor or, in other words, the higher the z-score, the higher the indicator value of a given species. The higher the z-score, the darker the red or gray color (for low values it is light blue). The function also generates black vertical lines on the graph. These are the so-called threshold values, which tell us where on the gradient there is a sharp change (an increase in increasers or a decrease in decliners) in the abundance of a given species.

Finally, we used Generalized Linear Mixed-Effect Models (GLMMs), using the `glmmTMB` package (Brooks et al. 2017), with Poisson or negative binomial family distribution, to exactly determine the relationships between the abundance of seedlings and saplings of each species with invader aboveground biomass. To test the invasional meltdown hypothesis, we also evaluated the relationships between the abundance of saplings of invasive species (excluding the dominant invader whose effects we were exploring) and invader aboveground biomass. For saplings we created models for species that occurred in at least 20% of the plots in a given variant (invader and habitat type) (Suppl. material 1: table S4). For seedlings we developed models for species that occurred in at least 10% of the plots in a given variant (invader and habitat type) (Suppl. material 1: table S13). In the Results section we present only statistically significant results (with $p < 0.05$). We used the DHARMA package (Hartig 2022) to conduct formal zero inflation and dispersion tests for each model. We started from models assuming Poisson distributions, due to the count character of our data. If we did not find problems with overdispersion we tested zero inflation, and in the case of statistically significant zero inflation, we used zero-inflated Poisson distribution. If we found statistically significant overdispersion we used negative binomial distribution, adding zero-inflation when necessary. We used invader aboveground biomass and stand age as fixed continuous effects and forest district and the year of natural regeneration assessment as random intercept, to cover spatial and temporal dependence within our dataset. We used the `dredge()` function of the MuMIn package (Bartoń 2017) to choose the best model according to comparing Akaike's Information Criterion of null model $AICc_0$ with the final model $AICc$. We presented the results using marginal responses implemented in the `ggpredict()` function from the `ggeffects` package (Lüdtke 2018). These responses show mean model prediction for each level of predictor, assuming remaining predictors at a constant (mean) level, and excluding random effects (prediction for global population). We excluded two outlying observations in the model of *Cerasus avium* saplings density for *R. pseudoacacia* in rich sites (densities: 304 and 37 ind.) and one in the model of *Carpinus betulus* saplings density for *P. serotina* rich sites (density: 1206 ind.). In these plots very high regeneration density resulted from an abundance of propagule pressure in proximity and did not allow for developing models reflecting overall conditions. We used the `ggplot2` package (Wickham 2016) to present results on the graphs. In the results, we provide extreme values of sapling density for some species, i.e. zero and a value close to the maximum of the gradient for *R. pseudoacacia* and *P. serotina* in individual habitats. All mean values are followed by \pm SD, except \pm SE in the results of GLMMs.

Results

Within 160 plots, we recorded 56 woody plant species in the saplings, including 12 alien species. For seedlings, we recorded 21 woody plant species, including four alien species. We counted from 5 to 2594 saplings on particular plots with an average of 142 ± 270 individuals. We counted from 0 to 243 seedlings on particular plots with an average of 13 ± 35 individuals. The stand age on our plots varied from 42 to 139 years old for *Quercus* spp. stands and from 42 to 117 years old for *P. sylvestris* stands. The mean total aboveground biomass for nutrient-poor sites with *P. sylvestris* was very similar between control plots ($187.17 \pm 34.50 \text{ Mg ha}^{-1}$) and plots with *P. serotina* ($196.99 \pm 33.25 \text{ Mg ha}^{-1}$) and *R. pseudoacacia* ($182.14 \pm 31.44 \text{ Mg ha}^{-1}$). In the case of the *Quercus* spp. stands the average total aboveground biomass of the control stand ($278.74 \pm 100.16 \text{ Mg ha}^{-1}$) was similar to the stand with *P. serotina* ($267.52 \pm 93.24 \text{ Mg ha}^{-1}$) but stands with *R. pseudoacacia* ($317.01 \pm 141.48 \text{ Mg ha}^{-1}$) had slightly higher biomass (Table 1). The differences between *P. serotina* and *R. pseudoacacia* were visible in their biomass. For *P. serotina* we reached aboveground biomass from 0.18 to 47.11 Mg ha^{-1} with an average of $7.34 \pm 8.75 \text{ Mg ha}^{-1}$ on nutrient-poor sites with *P. sylvestris* and from 0.19 to 27.39 Mg ha^{-1} with an average of $6.68 \pm 7.24 \text{ Mg ha}^{-1}$ on nutrient-rich sites with *Quercus* spp. For *R. pseudoacacia*, we reached aboveground biomass from 0.22 to 153 Mg ha^{-1} with an average of $20.91 \pm 31.69 \text{ Mg ha}^{-1}$ on nutrient-poor sites with *P. sylvestris* and from 0.82 to $278.24 \text{ Mg ha}^{-1}$ with an average of $50.77 \pm 70.37 \text{ Mg ha}^{-1}$ on nutrient-rich sites with *Quercus* spp. (Table 1, Fig. 4). *Prunus serotina* occurred only in the understory and subcanopy layers. The largest measured individual of *P. serotina* reached a DBH of 31.1 cm and a height of 19.0 m. *Robinia pseudoacacia* occurred in the understory, subcanopy, and canopy layers. The largest *R. pseudoacacia* individuals reached a DBH of 64.2 cm and a height of 32.0 m.

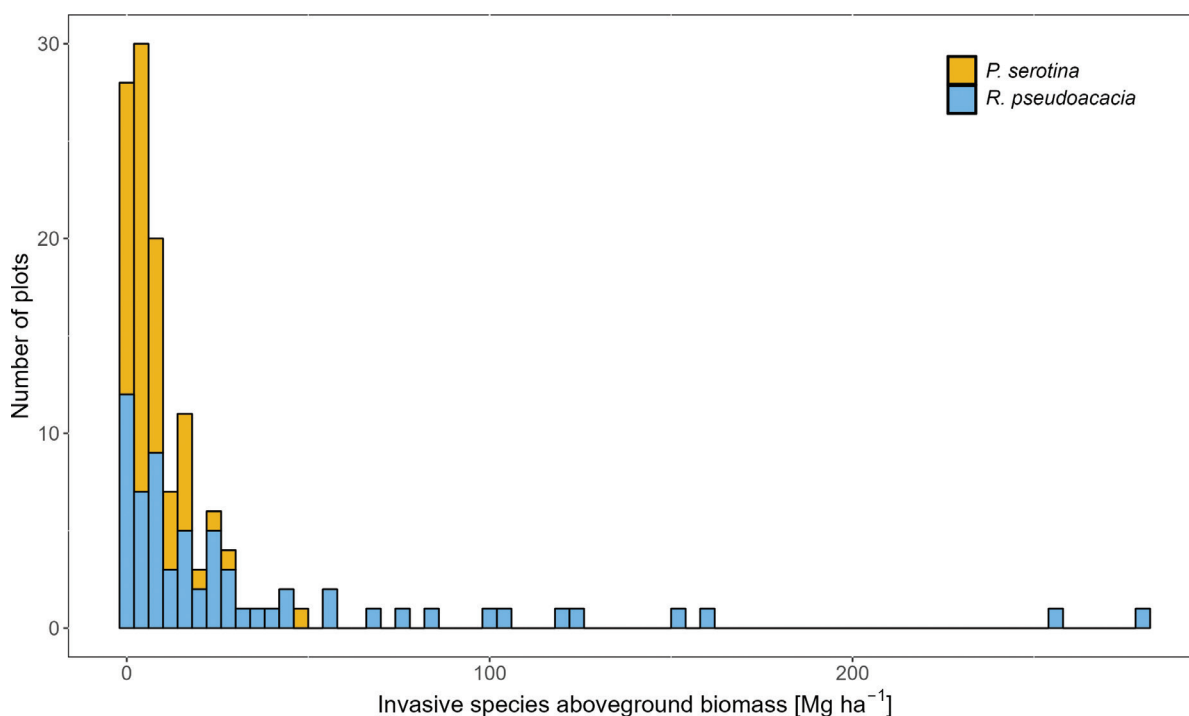


Figure 4. Histogram showing the distribution of invasive species aboveground biomass [Mg ha^{-1}] in plots with *P. serotina* ($n = 64$), and plots with *R. pseudoacacia* ($n = 64$). In this graph we excluded control plots ($n = 32$) with no studied invasive species for clarity.

Relationship between the biomass of invasive trees on species composition the natural regeneration species composition (CCA)

Species composition depended on invader biomass, both for stands with *P. serotina* and *R. pseudoacacia*, and both on the nutrient-rich and nutrient-poor sites. The stand age was statistically significant for *R. pseudoacacia* on nutrient-poor ($p = 0.004$ Fig. 5, Table 2) and nutrient-rich sites ($p = 0.034$). *Prunus serotina* biomass was positively correlated with the frequency of *Sorbus aucuparia*, *P. serotina*, *Fagus sylvatica*, and *Q. robur* on nutrient-poor sites, and *A. platanoides*, *Fraxinus excelsior*, *Q. robur*, *Prunus cerasifera*, *Prunus padus*, *P. serotina*, *F. alnus*, *U. minor* and *Sambucus nigra* on nutrient-rich sites. *Robinia pseudoacacia* biomass was positively correlated with *S. aucuparia*, *R. pseudoacacia*, and *S. nigra* on nutrient-poor sites, and *R. pseudoacacia*, *A. platanoides*, *Acer campestre*, *Acer pseudoplatanus*, *U. minor*, *F. alnus*, *P. serotina*, *P. cerasifera*, *C. avellana*, *Euonymus europaeus*, and *S. nigra* on nutrient-rich sites (Fig. 5).

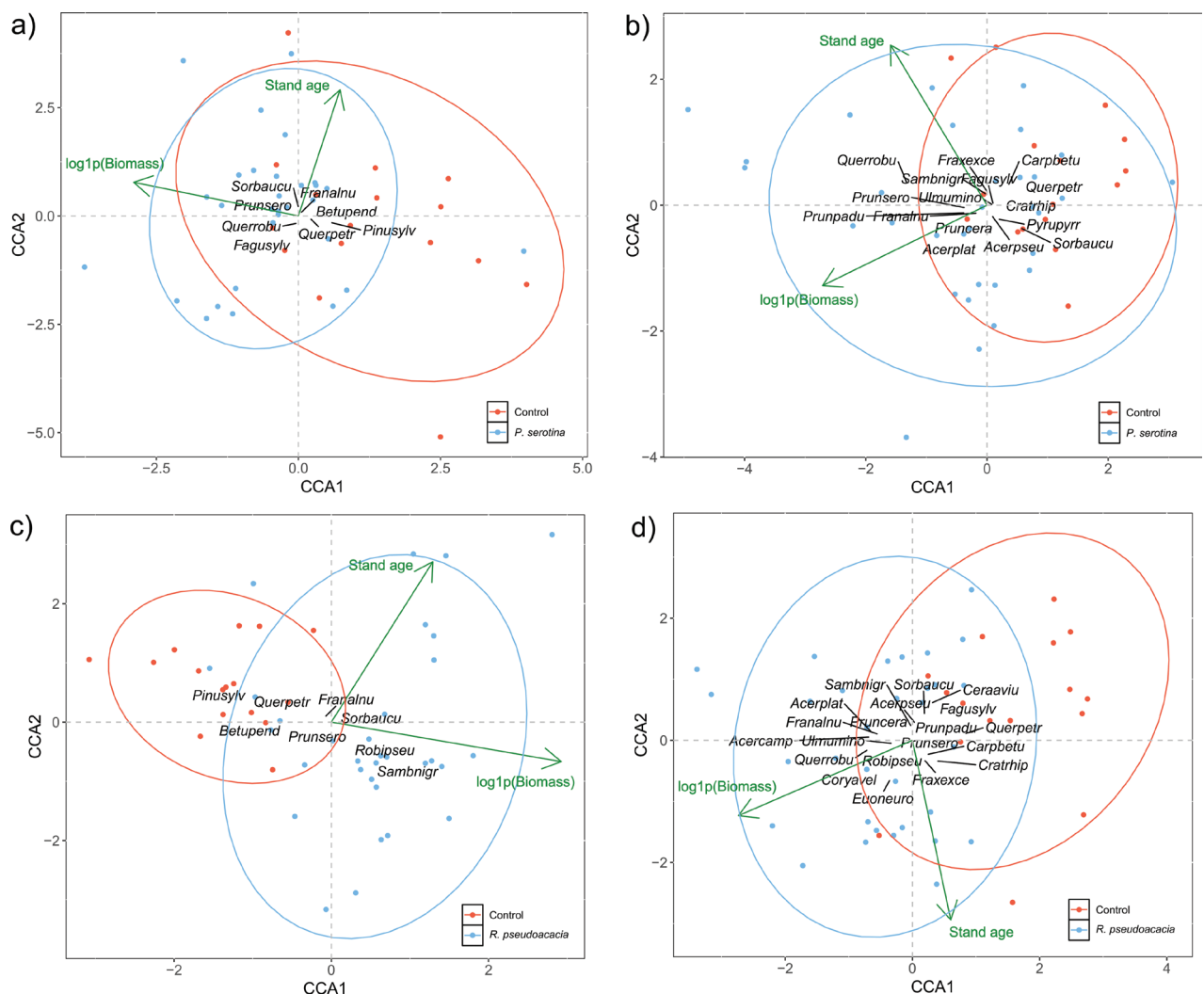


Figure 5. Canonical Correspondence Analysis (CCA) for **a** nutrient-poor sites with *P. serotina* ($n = 47$ plots) **b** nutrient-rich sites with *P. serotina* ($n = 48$ plots) **c** nutrient-poor sites with *R. pseudoacacia* ($n = 48$ plots) **d** nutrient-rich sites with *R. pseudoacacia* ($n = 48$ plots). Species with a frequency $> 20\%$ are labeled. Green arrows and green labels represent environmental variables. Red dots = control plots, light blue dots = plots with *P. serotina* or *R. pseudoacacia*. Abbreviations: log1p(Biomass) — natural logarithm of invader aboveground biomass.

Table 2. Results of permutation-based ANOVA-like test (999 iterations) of constraints significance for CCA. Abbreviations: log1p(Biomass) — natural logarithm of invader aboveground biomass.

| | Df | χ^2 | F | Pr(>F) |
|---|----|----------|--------|--------|
| <i>P. serotina</i> nutrient-poor sites (n = 47 plots) | | | | |
| log1p(Biomass) | 1 | 0.0791 | 1.6678 | 0.038 |
| Stand age | 1 | 0.0552 | 1.1635 | 0.376 |
| Residual | 44 | 2.0870 | | |
| <i>P. serotina</i> nutrient-rich sites (n = 48 plots) | | | | |
| log1p(Biomass) | 1 | 0.1446 | 1.9633 | 0.005 |
| Stand age | 1 | 0.1048 | 1.4232 | 0.119 |
| Residual | 45 | 3.3133 | | |
| <i>R. pseudoacacia</i> nutrient-poor sites (n = 48 plots) | | | | |
| log1p(Biomass) | 1 | 0.2372 | 3.1398 | 0.001 |
| Stand age | 1 | 0.1725 | 2.2833 | 0.004 |
| Residual | 45 | 3.3991 | | |
| <i>R. pseudoacacia</i> nutrient-rich sites (n = 48 plots) | | | | |
| log1p(Biomass) | 1 | 0.1753 | 2.3626 | 0.001 |
| Stand age | 1 | 0.1201 | 1.6184 | 0.034 |
| Residual | 45 | 3.3382 | | |

Abbreviations: Df – degrees of freedom; χ^2 – Chi-squared statistics; F – F-statistics; Pr(>F) – p-values.

Threshold Indicator Taxa Analysis

For *P. serotina*, we observed similar trends on both nutrient-poor and nutrient-rich sites (Fig. 6a, b, Suppl. material 1: tables S5, S6). The analysis revealed that *Q. petraea* saplings density declined with increasing *P. serotina* biomass and the opposite trend for *P. serotina* saplings. In the stands with *R. pseudoacacia*, more species revealed any response (Fig. 6c, d, Suppl. material 1: tables S7, S8). The decliners were *Pinus sylvestris*, *Q. petraea*, and *B. pendula* on nutrient-poor sites and *Q. petraea* on nutrient-rich sites. On the nutrient-poor sites *S. nigra*, *P. padus*, *A. platanoides*, and *R. pseudoacacia* increased their saplings density with increasing *R. pseudoacacia* biomass. On the nutrient-rich sites *A. platanoides*, *Q. robur*, and *R. pseudoacacia* increased their saplings density with increasing *R. pseudoacacia* biomass (Fig. 6c, d, Suppl. material 1: tables S7, S8).

Generalized linear mixed-effect models (GLMMs)

Prunus serotina on nutrient-poor sites

The density of all alien species saplings (without *P. serotina*) decreased from 2.3 ± 1.3 in control plots to 0.2 ± 1.3 in stands with 16 Mg ha^{-1} of *P. serotina*. Three species decreased their density with increasing *P. serotina* aboveground biomass. We found the highest effect size for *Q. petraea*. The number of individuals decreased from 24.3 ± 0.3 in control plots to 9.9 ± 0.4 in stands with 16 Mg ha^{-1} of *P. serotina*. *Pinus sylvestris* and *Q. robur* also reacted negatively but with smaller effect sizes. *Pinus sylvestris* individuals decreased from 1.7 ± 1.2 in control plots to 0.4 ± 1.2 in stands with 16 Mg ha^{-1} of *P. serotina*. *Quercus robur* individuals decreased from 0.7 ± 2.2 in control plots to 0.0 ± 2.3 in stands with 16 Mg ha^{-1} of *P. serotina*. Three species increased their density with increasing *P. serotina* aboveground biomass. *Prunus serotina* regenerated the best. The number of its individuals increased from

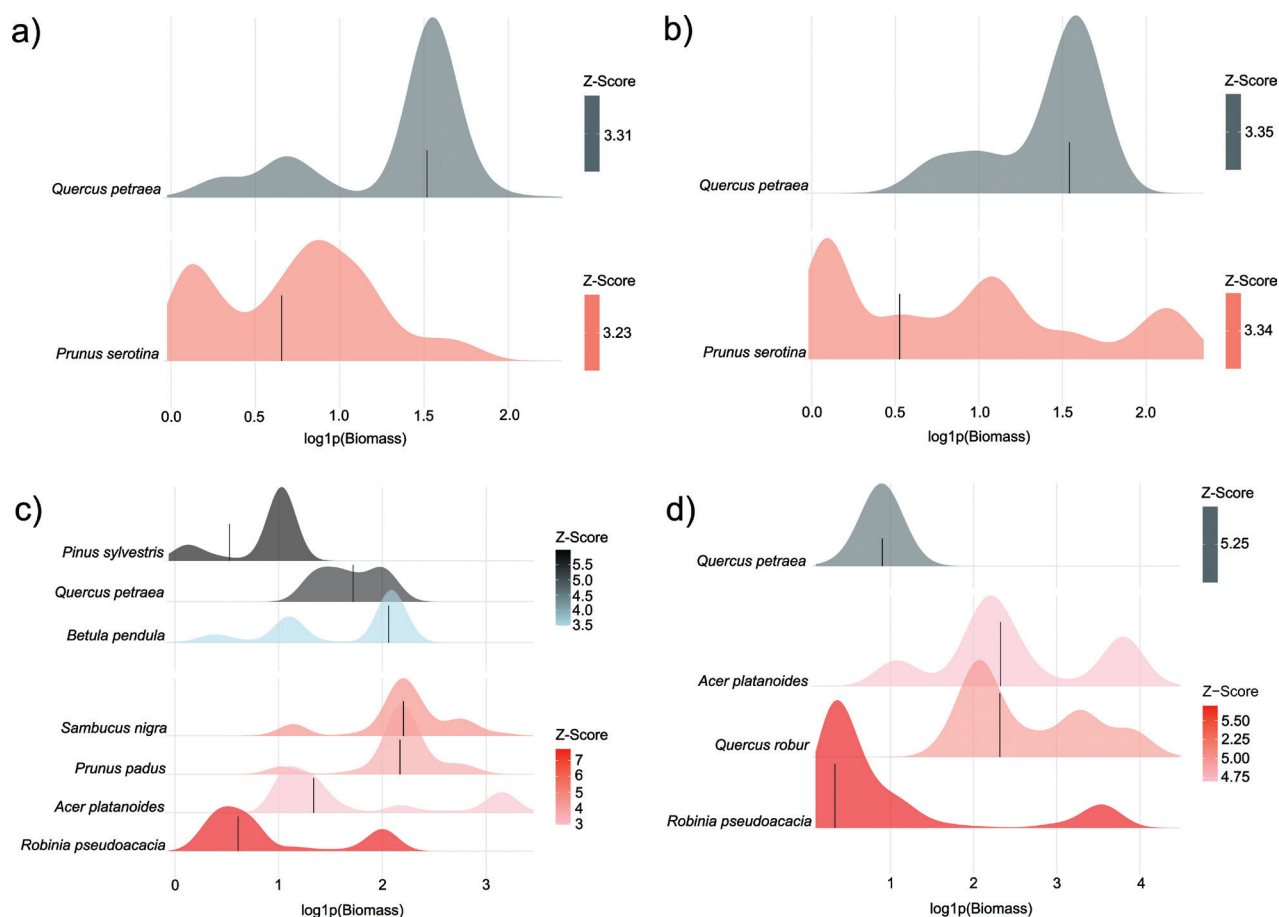


Figure 6. Results of Threshold Indicator Taxa Analysis (see Methods section for interpretation of the graph) for **a** nutrient-poor sites with *P. serotina* (n = 47 plots) **b** nutrient-rich sites with *P. serotina* (n = 48 plots) **c** nutrient-poor sites with *R. pseudoacacia* (n = 48 plots) **d** nutrient-rich sites with *R. pseudoacacia* (n = 48 plots). Grey/blue density estimators represent species responding negatively to invader biomass gradient (decliners) while red color – positively (increasers). We included here only responses for species that were both reliable (reliability ≥ 0.95) and pure (purity ≥ 0.95). For statistics of all species see Suppl. material 1: tables S5–S8.

10.0 \pm 0.3 in control plots to 275.6 \pm 0.3 in stands with 16 Mg ha⁻¹ of *P. serotina*. The other increasers were *S. aucuparia* and *B. pendula* (Table 3, Suppl. material 1: table S9, Fig. 7). We found an increasing number of *P. serotina* and *Q. petraea* seedlings and decreasing number of *P. sylvestris* seedlings with an increase in *P. serotina* aboveground biomass (Table 3, Suppl. material 1: table S14, Fig. 8).

Prunus serotina on nutrient-rich sites

Saplings of two species decreased their density with increasing *P. serotina* aboveground biomass. We observed the highest effect size for *Q. petraea*. The number of individuals decreased from 3.5 \pm 2.0 in control plots to 0.2 \pm 2.0 in stands with 28 Mg ha⁻¹ of *P. serotina*. *Carpinus betulus* was the second decliner, but with a lower effect size. The number of individuals decreased from 1.3 \pm 0.8 in control plots to 0.6 \pm 0.8 in stands with 28 Mg ha⁻¹ of *P. serotina*. Four species increased their density with increasing *P. serotina* aboveground biomass. Similarly to the nutrient-poor sites, *P. serotina* regenerated the best. The number of individuals increased from 2.5 \pm 0.6 in control plots to 90.0 \pm 0.6 in stands with 28 Mg ha⁻¹ of *P. serotina*. The other increasers, but with lower effect sizes, were *F. excelsior*, *U. minor*, and *P. padus* (Table 4, Suppl. material 1: table S10,

Fig. 9). We found an increasing number of *P. serotina* and *A. pseudoplatanus* seedlings with an increase in *P. serotina* aboveground biomass (Table 4, Suppl. material 1: table S15, Fig. 10).

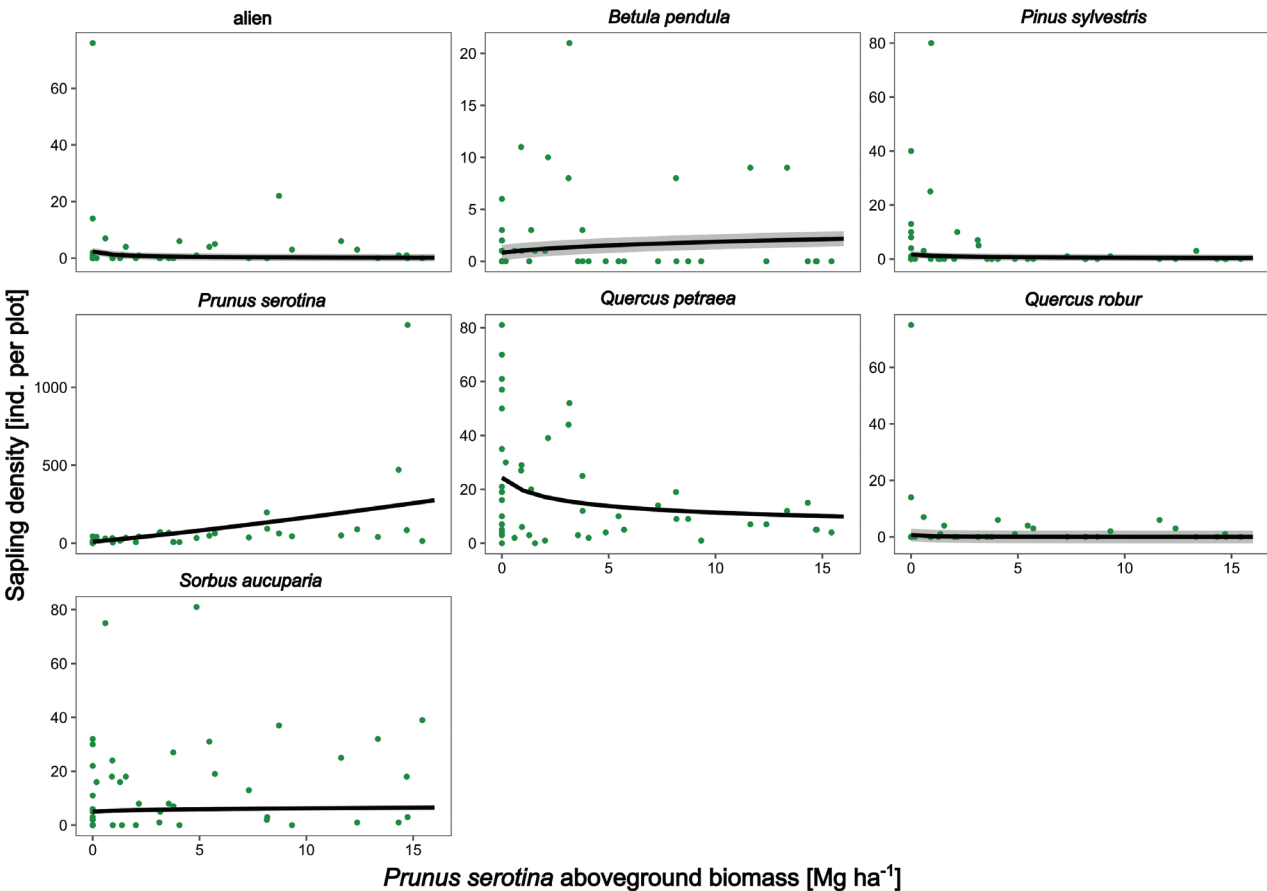


Figure 7. Generalized linear mixed-effect models for sapling density [ind. per plot] of particular species depending on *Prunus serotina* aboveground biomass [Mg ha⁻¹] in nutrient-poor sites. Dark green dots — observed values, black line — marginal responses, grey area — marginal responses ± standard error, alien — density of all alien species saplings excluding *P. serotina*.

Table 3. Predictions of natural regeneration density [ind. per plot] along *P. serotina* aboveground biomass gradient on the nutrient-poor sites, estimated using Generalized Linear Mixed-effect Models. The predicted values are marginal responses from models (Suppl. material 1: tables S9, S14), assuming constant (mean) stand age and excluding random effects.

| Species | <i>P. serotina</i> aboveground biomass [Mg ha ⁻¹] | | | | | | | | | |
|---|---|-----|----------|-----|----------|-----|----------|-----|----------|-----|
| | 0 | | 2 | | 6 | | 10 | | 16 | |
| | Estimate | SE | Estimate | SE | Estimate | SE | Estimate | SE | Estimate | SE |
| SAPLINGS | | | | | | | | | | |
| All alien species (without <i>P. serotina</i>) | 2.3 | 1.3 | 0.8 | 1.3 | 0.4 | 1.3 | 0.3 | 1.3 | 0.2 | 1.3 |
| <i>Quercus petraea</i> | 24.3 | 0.3 | 17.2 | 0.3 | 13.1 | 0.3 | 11.4 | 0.3 | 9.9 | 0.4 |
| <i>Quercus robur</i> | 0.7 | 2.2 | 0.1 | 2.2 | 0.0 | 2.2 | 0.0 | 2.2 | 0.0 | 2.3 |
| <i>Pinus sylvestris</i> | 1.7 | 1.2 | 1.0 | 1.2 | 0.6 | 1.2 | 0.5 | 1.2 | 0.4 | 1.2 |
| <i>Prunus serotina</i> | 10.0 | 0.3 | 36.2 | 0.2 | 97.6 | 0.2 | 165.6 | 0.2 | 275.6 | 0.3 |
| <i>Sorbus aucuparia</i> | 5.1 | 0.7 | 5.6 | 0.7 | 6.0 | 0.7 | 6.3 | 0.7 | 6.5 | 0.7 |
| <i>Betula pendula</i> | 0.8 | 0.8 | 1.2 | 0.7 | 1.6 | 0.7 | 1.9 | 0.7 | 2.2 | 0.7 |
| SEEDLINGS | | | | | | | | | | |
| <i>Prunus serotina</i> | 1.2 | 1.1 | 3.6 | 1.1 | 8.2 | 1.1 | 12.9 | 1.1 | 19.7 | 1.1 |
| <i>Pinus sylvestris</i> | 1.0 | 0.6 | 0.7 | 0.6 | 0.5 | 0.6 | 0.4 | 0.7 | 0.3 | 0.7 |
| <i>Quercus petraea</i> | 0.1 | 1.0 | 0.2 | 0.9 | 0.4 | 0.9 | 0.7 | 0.9 | 1.0 | 0.9 |

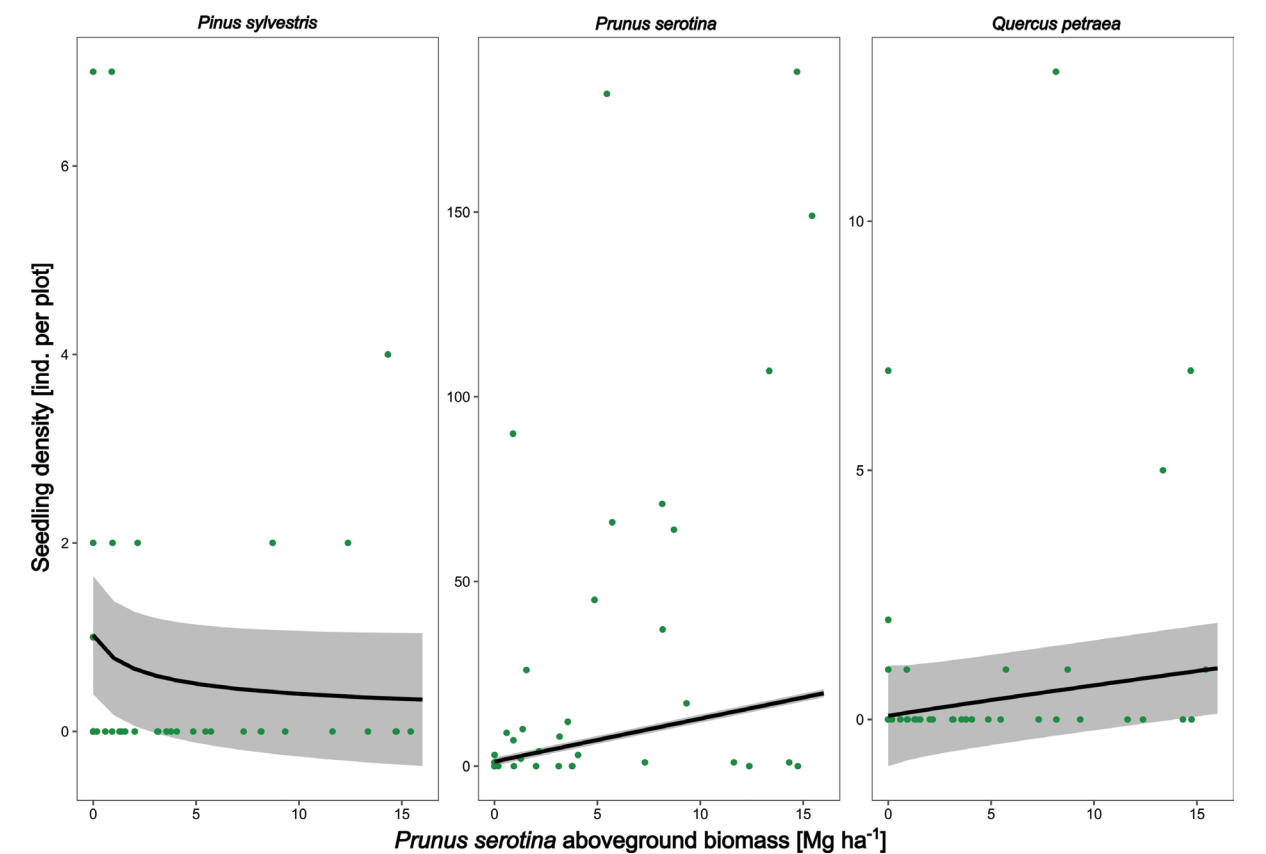


Figure 8. Generalized linear mixed-effect models for seedling density [ind. per plot] of particular species depending on *Prunus serotina* aboveground biomass [Mg ha⁻¹] in nutrient-poor sites. Dark green dots — observed values, black line — marginal responses, grey area — marginal responses ± standard error.

Table 4. Predictions of natural regeneration density [ind. per plot] along *P. serotina* aboveground biomass gradient on the nutrient-rich sites, estimated using Generalized Linear Mixed-effect Models. The predicted values are marginal responses from models (Suppl. material 1: tables S10, S15), assuming constant (mean) stand age and excluding random effects.

| Species | <i>P. serotina</i> aboveground biomass [Mg ha ⁻¹] | | | | | | | | | |
|----------------------------|---|-----|----------|-----|----------|-----|----------|-----|----------|-----|
| | 0 | | 4 | | 10 | | 18 | | 28 | |
| | Estimate | SE | Estimate | SE | Estimate | SE | Estimate | SE | Estimate | SE |
| SAPLINGS | | | | | | | | | | |
| <i>Quercus petraea</i> | 3.5 | 2.0 | 0.9 | 2.0 | 0.5 | 2.0 | 0.3 | 2.0 | 0.2 | 2.0 |
| <i>Carpinus betulus</i> | 1.3 | 0.8 | 0.9 | 0.8 | 0.7 | 0.8 | 0.6 | 0.8 | 0.6 | 0.8 |
| <i>Prunus serotina</i> | 2.5 | 0.6 | 13.7 | 0.6 | 31.9 | 0.6 | 57.2 | 0.6 | 90.0 | 0.6 |
| <i>Fraxinus excelsior</i> | 2.6 | 0.8 | 10.4 | 0.8 | 20.5 | 0.8 | 32.8 | 0.8 | 47.2 | 0.8 |
| <i>Ulmus minor</i> | 0.2 | 1.0 | 0.4 | 1.0 | 0.6 | 1.0 | 0.8 | 1.0 | 1.1 | 1.0 |
| <i>Prunus padus</i> | 0.3 | 1.0 | 1.7 | 1.0 | 3.9 | 1.0 | 6.9 | 1.0 | 10.9 | 1.0 |
| SEEDLINGS | | | | | | | | | | |
| <i>Prunus serotina</i> | 0.3 | 1.0 | 1.7 | 1.0 | 3.9 | 1.0 | 6.9 | 1.0 | 10.8 | 1.0 |
| <i>Acer pseudoplatanus</i> | 0.3 | 1.0 | 1.7 | 1.0 | 3.9 | 1.0 | 6.9 | 1.0 | 10.8 | 1.0 |

Robinia pseudoacacia on nutrient-poor sites

The number of all alien species saplings (without *R. pseudoacacia*) increased from 3.2 ± 0.3 in control plots to 21.3 ± 0.3 in stands with 116 Mg ha^{-1} of *R. pseudoacacia*. The number of *S. aucuparia* individuals increased from 7.8 ± 0.3 in control plots to 13.3 ± 0.3 in stands with 116 Mg ha^{-1} of *R. pseudoacacia*. The number of *Q. petraea* individuals decreased from 12.5 ± 0.5 in control plots to 0.9 ± 0.5 in stands with

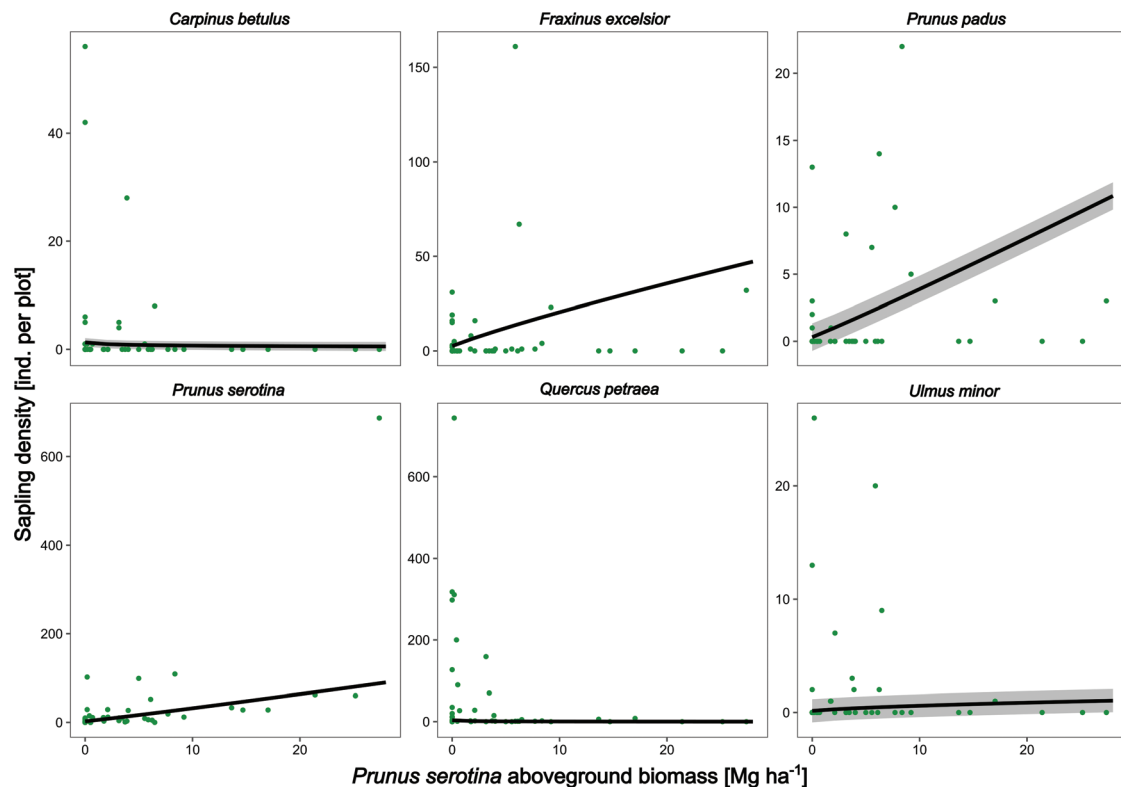


Figure 9. Generalized linear mixed-effect models for sapling density [ind. per plot] of particular species depending on *Prunus serotina* aboveground biomass [Mg ha^{-1}] in nutrient-rich sites. Dark green dots — observed values, black line — marginal responses, grey area — marginal responses \pm standard error.

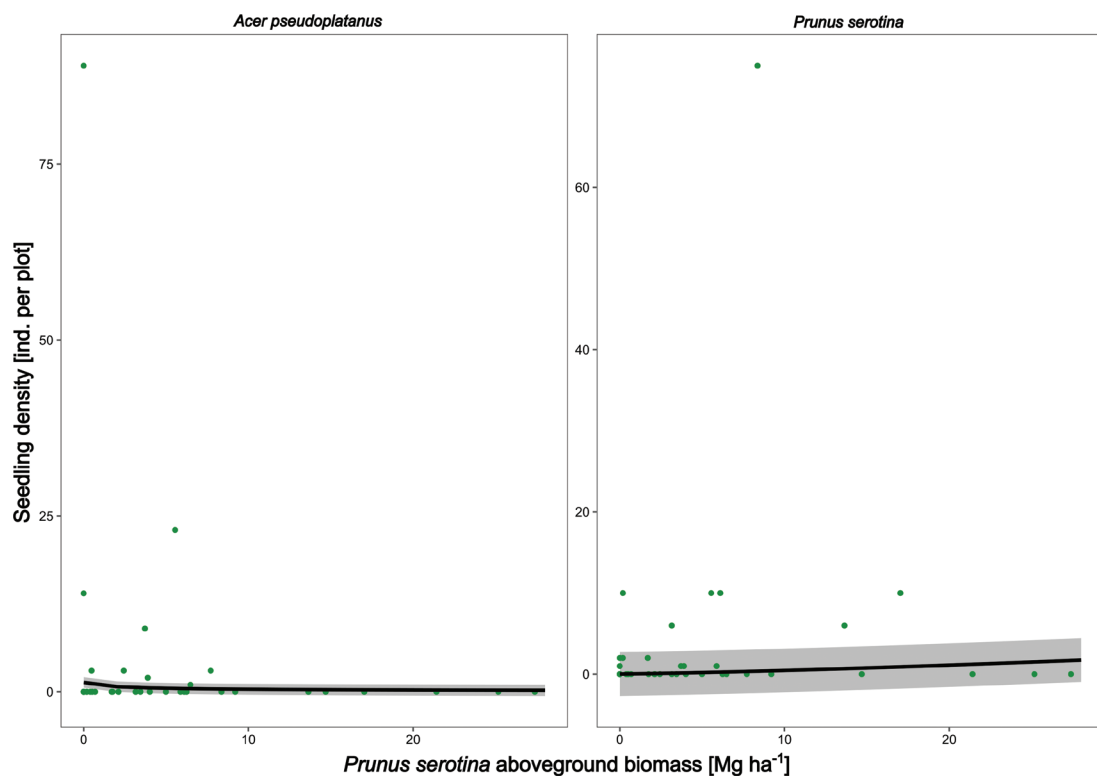


Figure 10. Generalized linear mixed-effect models for seedling density [ind. per plot] of particular species depending on *Prunus serotina* aboveground biomass [Mg ha^{-1}] in nutrient-rich sites. Dark green dots — observed values, black line — marginal responses, grey area — marginal responses \pm standard error.

116 Mg ha⁻¹ of *R. pseudoacacia*. For *R. pseudoacacia* saplings, we found significant results for the relationship with aboveground biomass for the zero-inflation model, showing that a higher quantity of *R. pseudoacacia* in the stand was negatively correlated with *R. pseudoacacia* regeneration (Estimate = -2.1411, $p < 0.001$) (Table 5, Suppl. material 1: table S11, Fig. 11). We found an increasing number of *R. pseudoacacia* seedlings and a decreasing number of *P. sylvestris* seedlings with an increase in *R. pseudoacacia* aboveground biomass (Table 5, Suppl. material 1: table S16, Fig. 12).

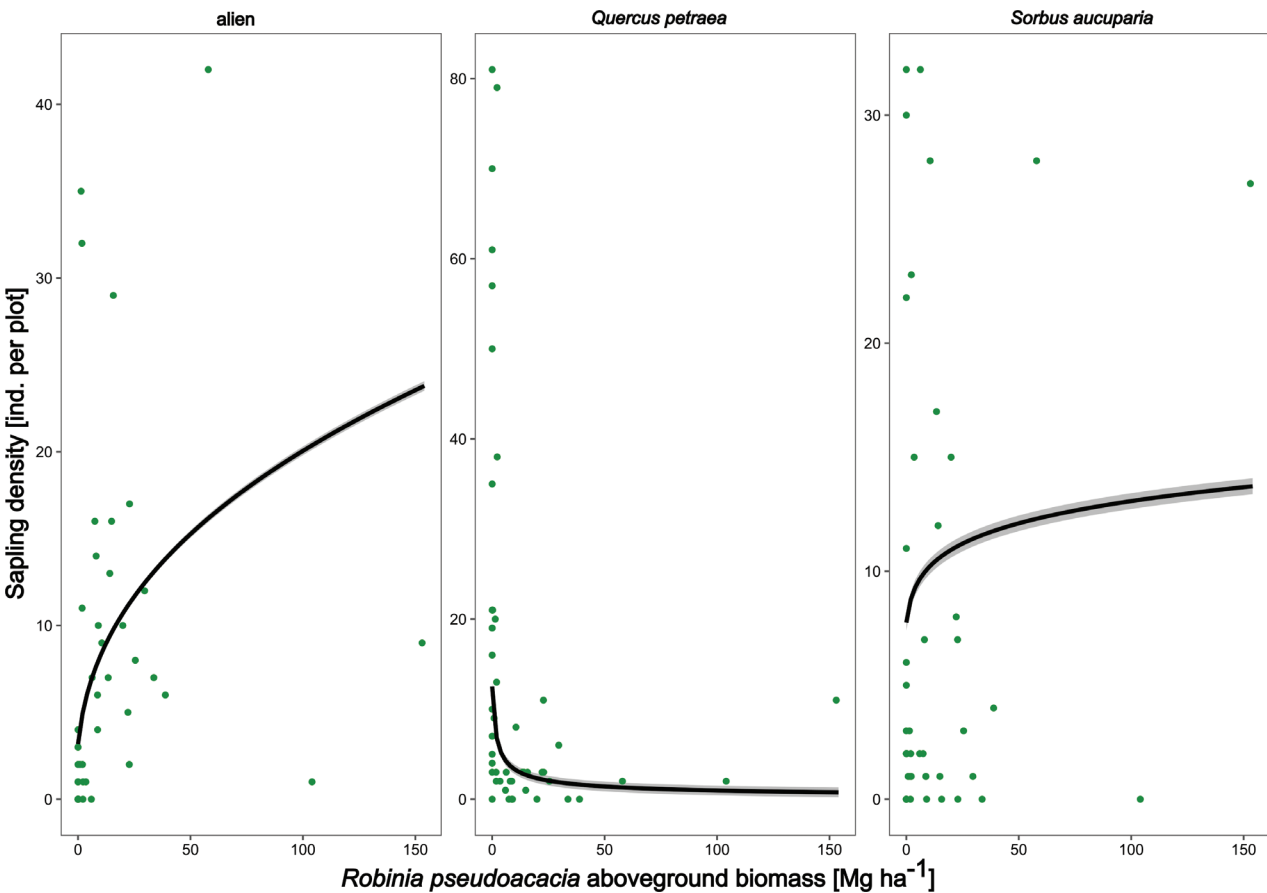


Figure 11. Generalized linear mixed-effect models for sapling density [ind. per plot] of particular species depending on *R. pseudoacacia* aboveground biomass [Mg ha⁻¹] in nutrient-poor sites. Dark green dots — observed values, black line — marginal responses, grey area — marginal responses \pm standard error, alien — density of all alien species saplings excluding *R. pseudoacacia*.

Table 5. Predictions of natural regeneration density [ind. per plot] along *R. pseudoacacia* aboveground biomass gradient on the nutrient-poor sites, estimated using Generalized Linear Mixed-effect Models. The predicted values are marginal responses from models (Suppl. material 1: tables S11, S16), assuming constant (mean) stand age and excluding random effects.

| Species | <i>R. pseudoacacia</i> aboveground biomass [Mg ha ⁻¹] | | | | | | | | | |
|---|---|-----|----------|-----|----------|-----|----------|-----|----------|-----|
| | 0 | | 20 | | 38 | | 78 | | 116 | |
| | Estimate | SE | Estimate | SE | Estimate | SE | Estimate | SE | Estimate | SE |
| SAPLINGS | | | | | | | | | | |
| All alien species (without <i>R. pseudoacacia</i>) | 3.2 | 0.3 | 10.7 | 0.2 | 13.7 | 0.2 | 18.2 | 0.2 | 21.3 | 0.3 |
| <i>Quercus petraea</i> | 12.5 | 0.5 | 2.3 | 0.5 | 1.7 | 0.5 | 1.1 | 0.5 | 0.9 | 0.5 |
| <i>Sorbus aucuparia</i> | 7.8 | 0.3 | 10.9 | 0.3 | 11.7 | 0.3 | 12.7 | 0.3 | 13.3 | 0.3 |
| SEEDLINGS | | | | | | | | | | |
| <i>Robinia pseudoacacia</i> | 0.0 | 2.0 | 0.1 | 2.0 | 0.2 | 2.0 | 0.4 | 2.0 | 0.5 | 2.0 |
| <i>Pinus sylvestris</i> | 0.2 | 1.2 | 0.1 | 1.2 | 0.1 | 1.2 | 0.1 | 1.3 | 0.1 | 1.3 |

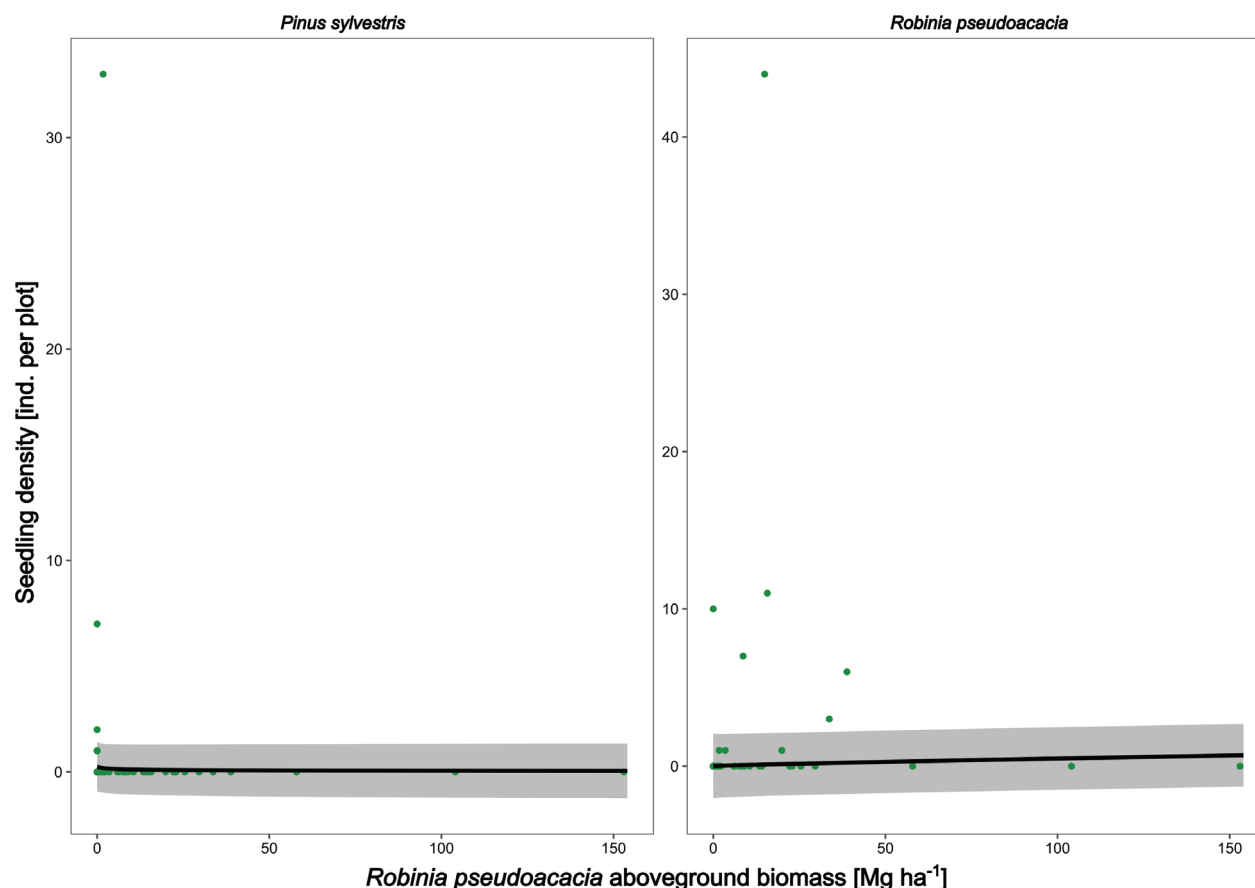


Figure 12. Generalized linear mixed-effect models for seedling density [ind. per plot] of particular species depending on *R. pseudoacacia* aboveground biomass [Mg ha^{-1}] in nutrient-poor sites. Dark green dots — observed values, black line — marginal responses, grey area — marginal responses \pm standard error.

Robinia pseudoacacia on nutrient-rich sites

The density of all alien species saplings (excluding *R. pseudoacacia*) increased from 2.8 ± 0.4 in control plots to 13.0 ± 0.4 in stands with 208 Mg ha^{-1} of *R. pseudoacacia*. Four species decreased their density, and 13 species increased their density with increasing *R. pseudoacacia* aboveground biomass. Mainly forest-forming species like *Q. petraea* and *F. sylvatica* decreased the density of saplings, while species occurring usually as an admixture in the stands (all native *Acer* spp., *F. excelsior*, and *U. minor*) and shrubs (*S. nigra*, *C. avellana*, *E. europaeus*, *Crataegus rhipidophylla*, and *F. alnus*) increased their saplings density with increasing *R. pseudoacacia* biomass. We found low negative effects of increasing *R. pseudoacacia* biomass on the saplings of *C. avium* and invasive *P. cerasifera*. Some of the species reached quite high effect sizes. The number of *Q. petraea* individuals decreased from 8.8 ± 0.8 in control plots to 0.1 ± 0.9 in stands with 208 Mg ha^{-1} of *R. pseudoacacia*. The number of *A. pseudoplatanus* individuals increased from 9.5 ± 0.6 in control plots to 36.9 ± 0.6 in stands with 208 Mg ha^{-1} of *R. pseudoacacia*. The number of *F. excelsior* individuals increased from 15.0 ± 0.7 in control plots to 36.8 ± 0.8 in stands with 208 Mg ha^{-1} of *R. pseudoacacia*. The number of *S. nigra* individuals increased from 1.8 ± 0.6 in control plots to 10.9 ± 0.6 in stands with 208 Mg ha^{-1} of *R. pseudoacacia* (Table 6, Suppl. material 1: table S12, Fig. 13). We found a decreasing number of *Q. petraea* and *A. pseudoplatanus* seedlings with an increase in *R. pseudoacacia* aboveground biomass (Table 6, Suppl. material 1: table S17, Fig. 14).

Table 6. Predictions of natural regeneration density [ind. per plot] along *R. pseudoacacia* aboveground biomass gradient on the nutrient-rich sites, estimated using Generalized Linear Mixed-effect Models. The predicted values are marginal responses from models (Suppl. material 1: tables S12, S17), assuming constant (mean) stand age and excluding random effects.

| Species | <i>R. pseudoacacia</i> aboveground biomass [Mg ha ⁻¹] | | | | | | | | | |
|---|---|-----|----------|-----|----------|-----|----------|-----|----------|-----|
| | 0 | | 34 | | 70 | | 138 | | 208 | |
| | Estimate | SE | Estimate | SE | Estimate | SE | Estimate | SE | Estimate | SE |
| SAPLINGS | | | | | | | | | | |
| All alien species (without <i>R. pseudoacacia</i>) | 2.8 | 0.4 | 7.8 | 0.3 | 9.5 | 0.3 | 11.6 | 0.4 | 13.0 | 0.4 |
| <i>Quercus petraea</i> | 8.8 | 0.8 | 0.4 | 0.8 | 0.2 | 0.8 | 0.1 | 0.9 | 0.1 | 0.9 |
| <i>Fagus sylvatica</i> | 1.0 | 0.6 | 0.2 | 0.6 | 0.2 | 0.7 | 0.1 | 0.8 | 0.1 | 0.8 |
| <i>Cerasus avium</i> | 0.5 | 1.1 | 0.0 | 1.3 | 0.0 | 1.4 | 0.0 | 1.5 | 0.0 | 1.5 |
| <i>Prunus cerasifera</i> | 0.4 | 2.6 | 0.1 | 2.6 | 0.1 | 2.6 | 0.1 | 2.6 | 0.1 | 2.6 |
| <i>Robinia pseudoacacia</i> | 1.1 | 0.7 | 2.7 | 0.7 | 3.1 | 0.7 | 3.7 | 0.7 | 4.1 | 0.7 |
| <i>Prunus serotina</i> | 0.6 | 0.6 | 2.8 | 0.6 | 3.8 | 0.6 | 5.1 | 0.6 | 6.1 | 0.6 |
| <i>Quercus robur</i> | 0.0 | 1.5 | 0.2 | 1.4 | 0.2 | 1.4 | 0.3 | 1.5 | 0.3 | 1.5 |
| <i>Acer pseudoplatanus</i> | 9.5 | 0.6 | 23.4 | 0.6 | 28.0 | 0.6 | 33.3 | 0.6 | 36.9 | 0.6 |
| <i>Acer platanoides</i> | 0.1 | 0.9 | 2.0 | 0.9 | 3.6 | 0.9 | 6.3 | 0.9 | 8.9 | 0.9 |
| <i>Acer campestre</i> | 0.1 | 2.4 | 0.4 | 2.4 | 0.5 | 2.4 | 0.7 | 2.4 | 0.9 | 2.4 |
| <i>Fraxinus excelsior</i> | 15.0 | 0.7 | 27.3 | 0.7 | 30.7 | 0.7 | 34.4 | 0.8 | 36.8 | 0.8 |
| <i>Ulmus minor</i> | 0.4 | 1.0 | 1.3 | 1.0 | 1.7 | 1.0 | 2.1 | 1.0 | 2.5 | 1.0 |
| <i>Sambucus nigra</i> | 1.8 | 0.6 | 6.0 | 0.6 | 7.6 | 0.6 | 9.5 | 0.6 | 10.9 | 0.6 |
| <i>Corylus avellana</i> | 0.2 | 0.5 | 0.9 | 0.3 | 1.2 | 0.4 | 1.6 | 0.4 | 1.9 | 0.4 |
| <i>Euonymus europaeus</i> | 0.0 | 1.1 | 0.4 | 1.1 | 0.5 | 1.0 | 0.8 | 1.1 | 1.1 | 1.1 |
| <i>Crataegus rhipidophylla</i> | 0.1 | 1.1 | 0.3 | 1.0 | 0.4 | 1.0 | 0.6 | 1.0 | 0.7 | 1.0 |
| <i>Frangula alnus</i> | 0.1 | 1.5 | 0.3 | 1.5 | 0.4 | 1.5 | 0.4 | 1.5 | 0.5 | 1.5 |
| SEEDLINGS | | | | | | | | | | |
| <i>Quercus petraea</i> | 0.1 | 1.8 | 0.0 | 1.8 | 0.0 | 1.8 | 0.0 | 1.9 | 0.0 | 1.9 |
| <i>Acer pseudoplatanus</i> | 0.6 | 1.5 | 0.1 | 1.5 | 0.0 | 1.5 | 0.0 | 1.6 | 0.0 | 1.6 |

Comparison of the methods

We used three different types of analyses, and in almost all cases we reached consistent results (Table 7). Among three tested methods we found the most consistent relationships for *Q. petraea* in all variants and *P. serotina* in plots with *P. serotina*. According to the Threshold Indicator Taxa Analysis, on the nutrient-poor sites with *P. serotina*, *B. pendula* were correlated negatively with the invader biomass, but according to the GLMMs positively. We found a contrast pattern in the case of *R. pseudoacacia* regeneration in stands with *R. pseudoacacia*, as TITAN2 suggested a positive relationship, but the model suggested a negative (but only for the zero-inflation component).

Discussion

General patterns

Observational studies on the impact of invasive species on various ecosystems, including forests, should not be considered as a simple causation based on observed correlations. Ecosystems are very complex and each of their elements is simultaneously affected by various factors. Impact assessment should be multidimensional and a systemic approach. In our plots we observed different densities of saplings and seedlings of individual species. We refer to individual hypotheses in the

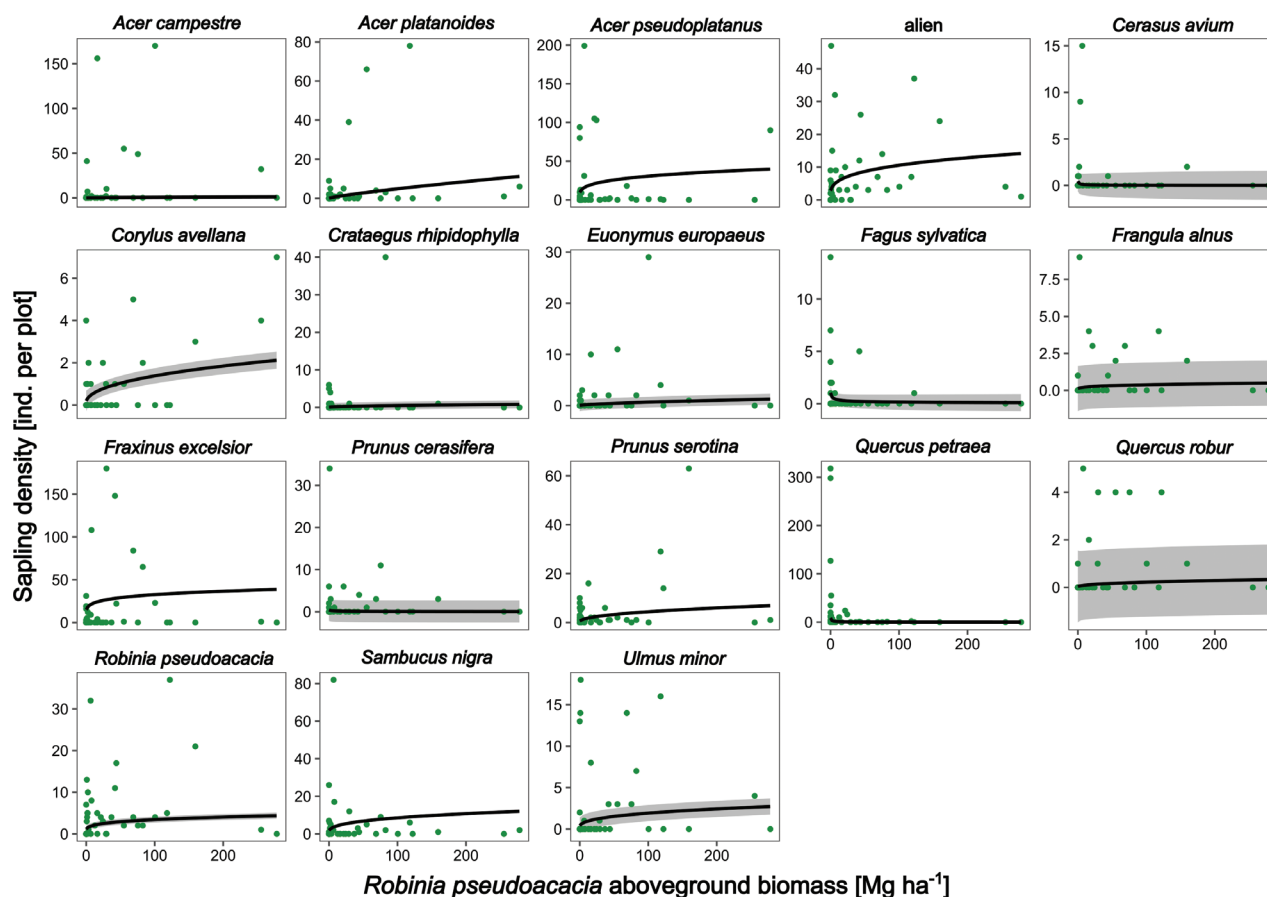


Figure 13. Generalized linear mixed-effect models for sapling density [ind. per plot] of particular species depending on *R. pseudoacacia* aboveground biomass [Mg ha^{-1}] in nutrient-rich sites. Dark green dots — observed values, black line — marginal responses, grey area — marginal responses \pm standard error, alien — density of all alien species saplings excluding *R. pseudoacacia*.

following sections of the discussion. The relationship between natural regeneration density and biomass of *P. serotina* and *R. pseudoacacia* can be both positive or negative, and this is in line with recent studies showing that results depend on the environmental context (Sapsford et al. 2020; Catford et al. 2022) and the reference ecosystem used for comparison (Sádlo et al. 2017; Medvecká et al. 2018; Dyderski and Jagodziński 2021b). Our study improves the knowledge about the relationship between different invasive tree biomasses and ecosystem services.

Species-specific patterns

We found different relationships between particular species natural regeneration densities and *R. pseudoacacia* and *P. serotina* biomasses (H1, H2). We confirm both the first (H1) and second (H2) hypotheses. The biomass of *R. pseudoacacia* was correlated with the density of natural regeneration more than *P. serotina* (H1). We also confirm the second hypothesis, as individual natural regeneration species showed different patterns of density. Some showed a decrease in density with the biomass increase of invaders, others showed opposite trends. Differences between individual species were seen in the number of individuals in each quantity of the invasive species, the shape (more linear or exponential), and the slope of the curves in the models. Similarly, in TITAN2, we found differences in the number of species and shapes of ridges (H2). Some natural regeneration species revealed

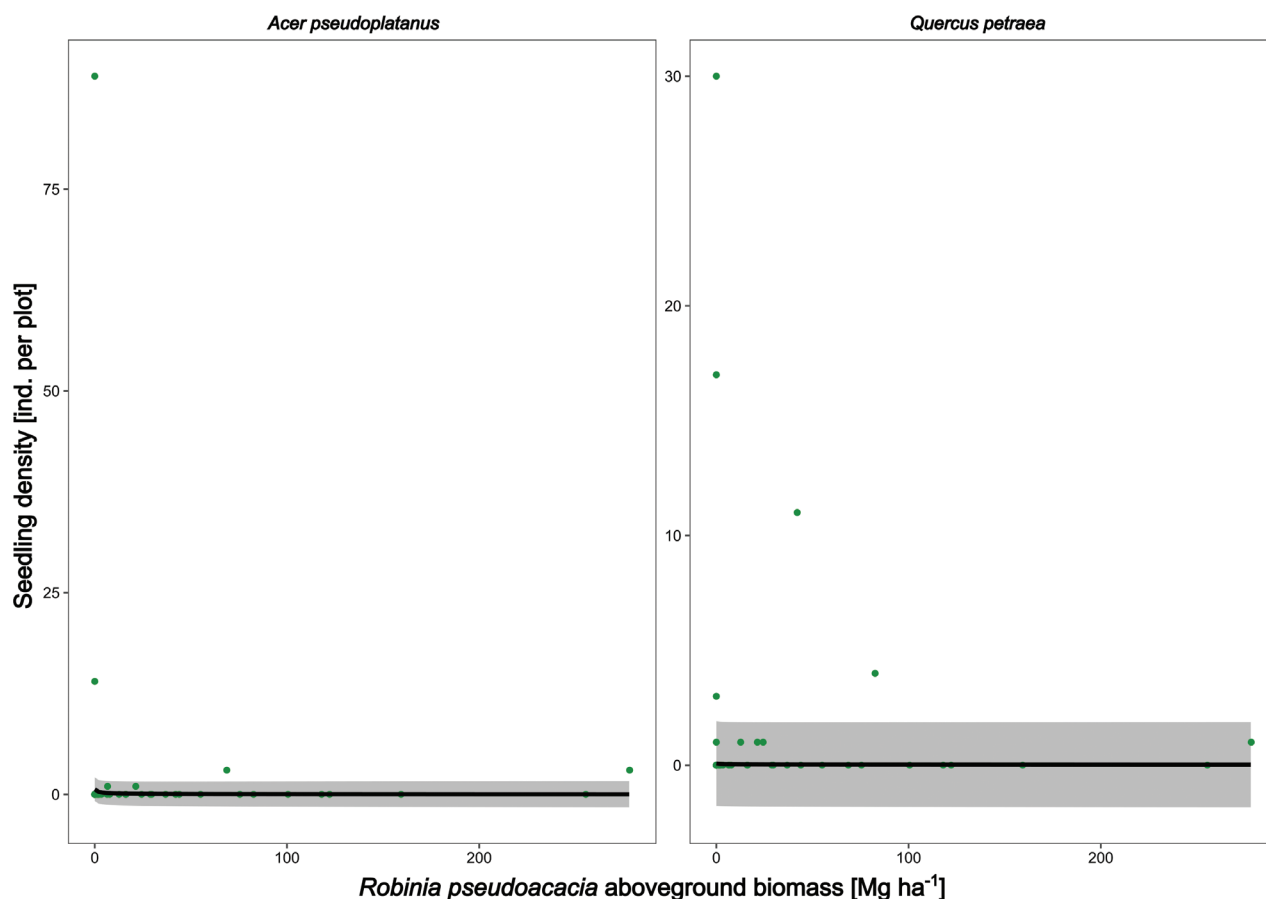


Figure 14. Generalized linear mixed-effect models for seedling density [ind. per plot] of particular species depending on *R. pseudoacacia* aboveground biomass [Mg ha⁻¹] in nutrient-rich sites. Dark green dots — observed values, black line — marginal responses, grey area — marginal responses \pm standard error.

positive relationships with invader biomass (mostly *P. serotina* in the stand with *P. serotina*) and some negative (*Q. petraea*, *P. sylvestris*). Those differences between particular species relationship with *R. pseudoacacia* or *P. serotina* should be mostly connected with different light or nutrient requirements of particular sapling and seedling species. As the transformations of both studied neophytes changed along their biomasses, also the density of particular natural regeneration species should change more intensively. There are visible trends connected with the ecological niches of particular trees, but they should be interpreted with caution. More shade-tolerant and nitrophilous species increased their abundances with invader biomass increasing, e.g., *F. excelsior* or *Acer* spp. In contrast, light-demanding and acidophilous *P. sylvestris* decreased its abundance or the abundance remained unchanged. Increasing biomass of either *P. serotina* or *R. pseudoacacia* led to reduced light availability on the forest floor and higher nutrient content in the soil (Rice et al. 2004; Dyderski and Jagodziński 2019; Engel et al. 2024). Those transformations did not support *P. sylvestris* regarding natural regeneration growth, in both saplings and seedlings. Lázaro-Lobo et al. (2021) also mentioned that the response of a particular species' natural regeneration depends on their functional traits, and the competition between invasive tree species with desirable species depends on their niche spacing. There are also visible differences in the number of significant relationships between sapling species densities and *R. pseudoacacia* or *P. serotina* biomasses (H1). Focusing only on GLMMs (Table 7), in nutrient-rich habitats

Table 7. Summary of saplings species' responses to invasive trees according to different analyses. CCA based on species with frequency > 20%, TITAN2 based on species with purity and reliability >= 0.95. GLMMs based on statistically significant results for the effect of invader aboveground biomass.

| | <i>Prunus serotina</i> | | | | | | <i>Robinia pseudoacacia</i> | | | | | |
|--------------------------------|------------------------|---|---|------------|---|---|-----------------------------|---|---|------------|---|---|
| | Poor sites | | | Rich sites | | | Poor sites | | | Rich sites | | |
| | C | T | M | C | T | M | C | T | M | C | T | M |
| <i>Acer campestre</i> | | | | | | | | | | + | | + |
| <i>Acer platanoides</i> | | | | + | | | | + | | + | + | + |
| <i>Acer pseudoplatanus</i> | | | | — | | | | | | + | | + |
| <i>Betula pendula</i> | — | | + | | | | — | — | | | | |
| <i>Corylus avellana</i> | | | | | | | | | | + | | + |
| <i>Cerasus avium</i> | | | | | | | | | | — | | — |
| <i>Carpinus betulus</i> | | | | — | | — | | | | — | | |
| <i>Crataegus rhipidophylla</i> | | | | — | | | | | | — | | + |
| <i>Euonymus europaeus</i> | | | | | | | | | | + | | + |
| <i>Frangula alnus</i> | — | | | + | | | + | | | + | | + |
| <i>Fraxinus excelsior</i> | | | | + | | + | | | | — | | + |
| <i>Fagus sylvatica</i> | + | | | ? | | | | | | — | | — |
| <i>Prunus cerasifera</i> | | | | + | | | | | | + | | — |
| <i>Prunus padus</i> | | | | + | | + | | + | | — | | |
| <i>Pyrus pyraeaster</i> | | | | — | | | | | | | | |
| <i>Prunus serotina</i> | + | + | + | + | + | + | — | | | — | | + |
| <i>Pinus sylvestris</i> | — | | — | | | | — | — | | | | |
| <i>Quercus petraea</i> | — | — | — | — | — | — | — | — | — | — | — | — |
| <i>Quercus robur</i> | + | | — | + | | | | | | + | + | + |
| <i>Robinia pseudoacacia</i> | | | | | | | + | + | — | + | + | + |
| <i>Sorbus aucuparia</i> | + | | + | — | | | + | | + | — | | |
| <i>Sambucus nigra</i> | | | | + | | | + | + | | + | | + |
| <i>Ulmus minor</i> | | | | + | | + | | | | + | | + |

Abbreviations: **C** — Canonical Correspondence Analysis (CCA); **T** — Threshold Indicator Taxa Analysis (TITAN2); **M** — Generalized Linear Mixed-Effect Models (GLMMs); **+** — positive effect of invasive species; **—** — negative effect of invasive species; **?** — unclear effect of invasive species.

17 species (13 positively and four negatively) responded significantly to *R. pseudoacacia* increasing biomass and six (four positively and two negatively) to *P. serotina* increasing biomass. In nutrient-poor habitats, three species (one positively and two negatively) responded to *R. pseudoacacia* increasing biomass and six (three positively and three negatively) to *P. serotina* increasing biomass. According to GLMMs in nutrient-rich habitats (*R. pseudoacacia*: 76%, *P. serotina*: 67%), the share of the number of species reacting positively to the invader's biomass in the number of species that responded significantly positively and negatively was higher than in coniferous habitats nutrient-poor habitats (*R. pseudoacacia*: 33%, *P. serotina*: 50%; H3).

For some species, we observed some trends similar to those observed by Dyderski and Jagodziński (2020), conducted in protected forests of the nearby Wielkopolska National Park. The density of forest tree species was lower in invaded stands by both *R. pseudoacacia* and *P. serotina* than in non-invaded while shrubs and admixed trees increased their density. Our study provided a significant advance from this study, as we included invader abundance, that allows for assessment of various stages of invasion (López-Núñez et al. 2017).

Our observations regarding the negative correlation between invasive trees biomass and the natural regeneration of forest-forming species are in line with the findings of Terwei et al. (2013) and Kowarik et al. (2019). Terwei et al. (2013)

showed that in the hardwood floodplain forests, *R. pseudoacacia* in the stand was positively correlated with the density of *R. pseudoacacia* seedlings. However, *P. serotina* in the stands was positively correlated with *P. serotina* seedlings but negatively with *U. minor* seedlings. Langmaier and Lapin (2020), in their review of the impact of different invasive plant species on forest regeneration, also discussed the impact of *P. serotina* and *R. pseudoacacia*. Based on the works of other authors (e.g., Rahmonov 2009; Maringer et al. 2012; Petrášová et al. 2013; Radtke et al. 2013; Terwei et al. 2013), Langmaier and Lapin (2020) synthesized the negative impact of *R. pseudoacacia* on species e.g., *Q. petraea*, *Q. robur*, *P. sylvestris*, *U. minor*. In our studies, we confirmed a negative correlation of *Q. petraea* and *P. sylvestris* regeneration density with invader biomass. For *Q. robur* and *U. minor*, we obtained less obvious positive responses. *Quercus robur* was less frequent than *Q. petraea* in our plots, while for *U. minor* we obtained significant results only for nutrient-rich sites. However, it should be borne in mind that their work accounted for habitats not only from Central Europe, but also other ecoregions, e.g., Western European deciduous forests, Pannonian mixed forests, or riparian forests.

Ambiguous invasional meltdown and propagule pressure hypotheses

When invasive species arrive in new niches, they can change soil chemicals, transform light conditions, and make the ecosystem more suitable for the other alien species (Crooks 2002; Corenblit et al. 2014; Jagodziński et al. 2024). In the longer term, this may increase the negative impact on biodiversity and other ecosystem services. For the total alien species natural regeneration density, we confirm the invasional meltdown hypothesis (H4) (Simberloff and Holle 1999) only for *R. pseudoacacia*, both on the nutrient-poor and nutrient-rich sites. Since we examined the relationship between *R. pseudoacacia* and *P. serotina* and the total density of all alien species in the regeneration layer, it is impossible to find species-specific patterns related to their biology and ecology. However, for some individual species we obtained significant results. *Prunus serotina* regeneration density was higher in plots with higher *R. pseudoacacia* biomass on nutrient-rich sites. However, little is known about the possible interactions between the adult *R. pseudoacacia* and *P. serotina* natural regeneration and vice versa. The interesting fact was that invasive *P. cerasifera* abundances decreased with an increase in *R. pseudoacacia* aboveground biomass. Due to the similar biology and ecology of this species to *P. serotina* we would expect rather similar responses. Czortek et al. (2024) proved that the presence of *P. cerasifera* natural regeneration is favored by higher light availability. However, this species avoids places with a higher number of functional types, which may indicate its lower resistance to competition than *P. serotina*.

According to the propagule pressure hypothesis, the higher the propagule pressure, the more effective colonization (Lonsdale 1999; Lockwood et al. 2005; Blackburn et al. 2011). This dependence of studied species on propagule pressure was confirmed in numerous previous studies (Vanhellemont et al. 2009; Vítková et al. 2017; Dyderski and Jagodziński 2018). Trees acquire reproductive abilities late. However, they retain these abilities for a very long time. More propagule sources should increase the regeneration capacity. We confirmed this hypothesis for *P. serotina* on both nutrient-rich and nutrient-poor sites, but the predicted values of sapling and seedling densities were higher on nutrient-poor sites. For *R. pseudoacacia*, we confirmed this hypothesis for saplings on nutrient-rich sites and seedlings

on nutrient-poor sites, but the predicted densities were low. In general, in our plots *R. pseudoacacia* did not regenerate as effectively as *P. serotina*. *Robinia pseudoacacia* spreads generatively mostly by wind and therefore prefers open spaces. *Prunus serotina* seeds mostly fall directly into the soil and to a lesser degree are spread by birds (Deckers et al. 2008; Vanhellemont et al. 2009; Dylewski et al. 2017). Also, both *P. serotina* (Starfinger et al. 2003) and *R. pseudoacacia* (Bouteiller et al. 2023) easily regenerate vegetatively by root suckers.

Dependence on habitat context and biotic resistance/acceptance

Biological invasion dynamics can depend on several factors: environmental conditions, interactions between species, anthropogenic factors, and management (González-Moreno et al. 2014; Sapsford et al. 2020; Catford et al. 2022). To exclude the management context, we established study plots in forest patches without visible impacts of silvicultural treatments e.g., planting or removing trees from plots. We also placed them in similar climatic conditions. We expected a more distinct decline in the density of natural regeneration to invader quantity/biomass on nutrient-poor than on nutrient-rich sites (H3) (Chmura 2004; Halarewicz 2011). In general, in nutrient-rich sites, there are higher densities of native trees understory, so the competition with invasive species is stronger. This is indicated by the number of species that reached a frequency > 20%. Comparing the abundances, *P. serotina* was more successful on nutrient-poor than nutrient-rich sites. Results for *P. serotina* are connected with the Empty Niche Hypothesis (Elton 1958; Schmitt 2020). This hypothesis suggests that invasive species can successfully settle new ecosystems by occupying weakly filled or unfilled ecological niches, where native species are less common or absent. In Central Europe, nutrient-poor sites with *P. sylvestris* have lower richness and abundance of native species compared to nutrient-rich habitats. *Prunus serotina* was massively introduced on nutrient-poor sites by foresters (Starfinger et al. 2003; Engel et al. 2024; Nyssen et al. 2024). Small competition from native trees facilitated the spread of *P. serotina* to new stands and led to their dominance in these habitats. This species further spreads easily to nearby stands. Especially, on nutrient-rich sites with *R. pseudoacacia*, we can observe that many of the native tree species regeneration increased their abundance with invader biomass increasing. More shade-tolerant species showed a positive correlation with invader biomass, except for *C. betulus* on nutrient-rich sites with *P. serotina*. This finding contradicts a previous study (Dyderski and Jagodziński 2020) revealing a positive response of this species to *P. serotina* presence. However, in the cited study, this response regarded *P. sylvestris* plantations on nutrient-rich sites, thus it cannot be directly compared. Our results balance between supporting the biotic acceptance (Stohlgren et al. 2006) and biotic resistance (Elton 1958; Levine et al. 2003) hypotheses. In the case of stands with *P. serotina*, both in poor and fertile habitats, the density of its regeneration increased with the biomass of the parental trees, mainly due to the availability of propagules and dispersal mechanisms: barochory and zoochory. Nevertheless, the effect sizes were higher on the poor sites. In the case of *R. pseudoacacia* stands, we observed slightly better regeneration of this species in nutrient-rich habitats. To sum up, for *P. serotina* our results are rather in line with the biotic resistance hypothesis (Elton 1958; Levine et al. 2003), while for *R. pseudoacacia* they rather in line with biotic acceptance (Stohlgren et al. 2006). The more visible relationships between natural regeneration and

invader biomass in nutrient-poor habitats depend on specific ecological conditions, specific plant species composition, and soil fertility. Therefore, any transformation by an invasive species is more severe for the species occurring there.

Three different analyses

We had to adapt the database to the analysis guidelines. CCA was the least conservative analysis in the case of input data. CCA is also the least sensitive on extremal observations. In models, we excluded one plot for *C. betulus* saplings and two plots for *C. avium* saplings (see the rationale in the Materials and Methods section). Thanks to the use of TITAN2, we were able to detect the threshold for particular invasion levels e.g., *P. serotina* saplings reacted quickly with big abundance on even small quantity of *P. serotina* in the stands, while *Q. petraea* as a decliner was more tolerant to *P. serotina* biomass increasing. For *C. avium* omitting these records in the models did not change the trend (positive/negative) but reduced the standard error and smoothed the regression curve. In the case of *C. betulus*, removing the extreme observation changed the trend from positive to negative. The negative trend is consistent with the CCA result. The extreme observation results from the fact that there were adult *C. betulus* in the vicinity of the plot, acting as a propagule source. According to the guidelines of statistical model development, we should remove this outlier. The model after removing the outlier had a more stable distribution of residuals and a lower standard error of estimates. Even though each of the analyses we use is based on slightly different data structures and responds differently to data variability, the results we obtain are very similar. In general, consistent responses revealed by three different methods suggest that all these tools are useful in the assessment of correlations with invasive species biomass. We also found that TITAN2 resulted in the most conservative approach – for *P. serotina* and *R. pseudoacacia* on nutrient-rich sites it revealed relationships only in the cases confirmed by two other methods. For *R. pseudoacacia* on nutrient-poor sites, it revealed relationships not confirmed by two other methods only for three species.

Wider context and management implications

In the context of current trends in forestry, *P. sylvestris* is still the main species in nutrient-poor sites areas, while *Quercus* spp. is in nutrient-rich sites. Therefore, referring to habitats studied here, densities of main forest-forming species were negatively correlated with the biomass of studied invasive species, especially *Q. petraea*. *Prunus serotina* also hindered the regeneration of *P. sylvestris* in the poor sites. We found an increasing density of *Quercus robur* saplings with increasing *R. pseudoacacia* biomass in fertile habitats, but negatively correlated with *P. serotina* biomass in poor habitats. In the context of natural forests and ongoing climate change, the situation looks a bit different. Wide-scale studies predict the retreat of forest-forming tree species from Central Europe, especially *P. sylvestris*, as a response to climate change (Dyderski et al. 2018; Chakraborty et al. 2021; Wessely et al. 2024). That way, studied neophytes can enhance this negative effect by suppressing the natural regeneration of studied species. Recent management strategies propose in some cases the assimilation of invasive species with native ecosystems (Nyssen et al. 2024), also for *P. serotina* (Nyssen and Vanhellemont 2016; Engel et al. 2024) and *R. pseudoacacia* (Sádlo et al. 2017). Such a strategy is recommended especially in fertile habitats that are biotically more resistant

to the development of invasion. In assimilating studied invasive species, managers should be hypersensitive to their potential impacts on main forest-forming species. When we want to maintain or increase the number of species such as *Q. petraea* in the regeneration, we should take into account the results of our research and apply methods that will facilitate their survival. Management in fertile habitats should be adapted to a long-term management plan. If we want to mimic natural processes, the presence of *R. pseudoacacia* (based on our research) may be helpful, as it promotes species such as *F. excelsior*, *U. minor*, or *Acer* spp. On the other hand, if we want to preserve as large a *Quercus* population as possible, some human action may be necessary. In the case of *P. sylvestris* stands, we maintain the fact that if we want successful *P. sylvestris* regeneration, it is necessary to take into account the observed decreasing density of *P. sylvestris* regeneration with both invasive species studied biomass increasing and support the regeneration of *P. sylvestris*. Langmaier and Lapin (2020) summarized that there are studies that indicate that in the case of *R. pseudoacacia*, its eradication measures or adaptation of silvicultural measures are the most frequent management actions, while in the case of *P. serotina* – early detection. The latter concerns both decision-makers and the entire society, because it is easier to control biological invasions in the early stages. In turn, silvicultural treatments can be modified to promote selective cutting, and appropriately manage the closure of tree crowns and density with local reduction of invasive species combined with the promotion of species of native origin. Unfortunately, our study revealed the negative correlations between studied invasive species biomass and the *Q. petraea* natural regeneration in poor sites. Due to changing climatic conditions leading to the retreat of coniferous species, many see the potential of *Q. petraea* to replace *P. sylvestris* (Hanewinkel et al. 2013; Dyderski et al. 2025). Since *R. pseudoacacia* and *P. serotina* are very common in European forests (Wagner et al. 2017; Campagnaro et al. 2018), and are predicted to expand their range under the changing climate (Puchałka et al. 2021, 2023), we may expect the negative impact on *Q. petraea* regeneration, that will require particular attention.

Although our study focused on managed forests, certain relationships can be related to natural forests. The areas we searched had the structure of semi-natural forests, managed in a way that imitated natural processes. In the case of protected forests, it is important to monitor the presence and impact of invasive species on natural processes and prevent possible damage they may cause. Eradication of invasive trees is expensive and sometimes counter-productive or even makes the situation worse (Namura-Ochalska and Borowa 2015; Nyssen and Vanhellemont 2016; Nyssen et al. 2024). Our study should be helpful for stakeholders in making decisions about the assimilation or eradication of invasive trees in particular types of stands on particular habitats (Nyssen and Vanhellemont 2016; Sádlo et al. 2017).

Conclusions

Our study provided the first quantitative assessment of the relationships between invasive tree biomass and forest natural regeneration, along the gradient of invader biomass. Additionally, we compared patterns obtained using three different statistical approaches: ordination, Threshold Indicator Taxa Analysis, and generalized linear mixed-effects models. We confirmed that invader taxa and their biomass are important and differentiate the strength of the relationship with natural regeneration. Additionally, we observed different relationships between nutrient-rich and nutrient-poor sites. Moreover, particular tree species were differently related to invader biomass on

particular sites and with different effect sizes. The most important finding is the negative relationship of studied invasive trees on the regeneration of crucial forest-forming tree species typical of the studied habitats, such as *P. sylvestris* in poor sites and *Q. petraea* in both nutrient-poor and rich sites. In general, *P. serotina* regenerated better than *R. pseudoacacia*, especially on nutrient-poor sites. For both species, we confirmed the importance of propagule pressure, expressed by parental tree biomass. We also confirmed the invasional meltdown hypothesis for stands with *R. pseudoacacia*, as the density of all non-native saplings (excluding *R. pseudoacacia*) increased with an increase in *R. pseudoacacia*. However, we did not confirm this hypothesis for stands with *P. serotina*. We also showed that three tested statistical approaches reveal consistent results, supporting the strength of our conclusions.

The results of our study are crucial for selecting tree species that regeneration is more vulnerable to studied invaders. This knowledge can improve the prioritization of management and designation of forest patches requiring additional silvicultural treatments to maintain or initiate natural regeneration. Moreover, our results allow determining thresholds of invasive biomass at which we observed a decreasing density of natural regeneration of the main tree species. For that reason, our study is important in the managed forests promoting natural regeneration, as well as for the protected forest areas e.g., national parks or forest reserves.

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Additional information

Conflict of interest

The authors declare no conflict of interest. The funders had no role in the design of the study; in the collection, analyses, or interpretation of data; in the writing of the manuscript, or in the decision to publish the results.

Ethical statement

No ethical statement was reported.

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Author contributions

Conceptualization: SB, MKD; methodology: SB, MKD; investigation: SB, MKD; formal analysis: SB; visualization: SB; writing—original draft preparation: SB; writing—review and editing: MKD; funding acquisition: MKD.

Author ORCIDs

Sebastian Bury  <https://orcid.org/0009-0006-5380-0521>

Marcin K. Dyderski  <https://orcid.org/0000-0003-4453-2781>

Data availability

All data supporting the results are archived in the figshare repository (Dyderski and Bury 2024) 10.6084/m9.figshare.26809084.

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Supplementary material 1

Supplementary information

Authors: Sebastian Bury, Marcin K. Dyderski

Data type: docx

Explanation note: This file contains supplementary details about natural regeneration species frequency, allometric models used to aboveground biomass calculation, and detailed data supporting the analyses presented in the manuscript

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