

Light can modify density-dependent seedling mortality in a temperate forest

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Abstract

Questions: There is growing evidence on how density-dependent drivers of plant performance are influenced by habitat heterogeneity such as variation in understorey light availability. How these processes operate in temperate forests still remains an open question, however. We examined the interactive effects of density dependence and light availability on woody seedling mortality across multiple species, two size stages and growth forms.

Location: Alluvial old-growth temperate forest, southeastern Czech Republic.

Methods: We mapped seedlings of woody species (≥ 10 cm tall) and recorded their mortality over a two-year period on 21 square seedling plots (25 m^2) within one large square plot with all trees mapped (≥ 1 cm diameter at breast height). Seedling mortality was studied using a combined approach of generalised linear mixed models and spatial point pattern analyses.

Results: Density-dependent effects of tree and seedling neighbours influenced seedling mortality at different spatial scales, depending on their size class, growth form and by taxon. Conspecific inhibition raised the mortality of seedlings other than *Acer campestre* at low light levels, indicating that host-specific enemies and/or intraspecific competition may be important in unfavourable habitats. While small seedlings experienced conspecific inhibition at low light levels, tall seedlings were additively affected by low-light conditions and competition with trees. Both conspecific and heterospecific neighbours tended to affect tree seedlings at low light levels, whereas shrub seedlings experienced light- and density-independent mortality. Some negative interspecific interactions indicated ongoing expansion of species like *Acer campestre* in currently flood-free habitats.

Conclusions: How density-dependent effects translate into demographic outcomes for woody seedling populations may be largely determined by variation in understorey light availability. Given that seedlings differ in size, growth form and taxa, we also demonstrate that both seedling and tree neighbours may contribute to the strength and spatial variation in density-dependent effects at seedling neighbourhood scales.

KEYWORDS

alluvial old-growth forest, density dependence, habitat heterogeneity, intraspecific competition, Janzen–Connell hypothesis, light availability, niche partitioning, seedling dynamics, spatial point patterns, species coexistence



1 | INTRODUCTION

Local biotic interactions such as intraspecific competition for resources and top-down interactions between plants acting as hosts and their specialised enemies (e.g. fungi, herbivores) may serve as drivers of diversity maintenance in a variety of ecosystems (Chesson, 2000; Adler et al., 2018). The negative effect of these interactions on the performance of plant populations (i.e. growth rate, survival) at high conspecific densities is referred to as conspecific negative density dependence. This density-dependent process is believed to play a key role in stabilising species coexistence (Janzen, 1970; Connell, 1971; Broekman et al., 2019).

Evidence is growing on how density-dependent effects and habitat heterogeneity, such as variation in light availability (McCarthy-Neumann & Ibañez, 2013; Uriarte et al., 2018) or topographic variation (Johnson et al., 2017; Fortunel et al., 2018), influence plant performance at plant neighbourhood scales (i.e. the spatial scales at which the focal plant can be directly or indirectly influenced by neighbouring plants). Understorey light availability is a prime example of an essential resource which provides niche differentiation among plant species at the earliest life stages, having direct and indirect positive effects on plant survival and recruitment (Muscolo et al., 2010; Diaci et al., 2012). From a different perspective, the susceptibility of seedlings to pathogens, defoliation and drought increases at low light levels due to stronger competition for resources (Dickie et al., 2005), increased virulence of pathogens and/or lower ability of plants to produce defences (Roberts & Paul, 2006; Liu & He, 2019). Such unfavourable environments may, on the other hand, have the benefit of less crowding from neighbouring plants (Zambrano et al., 2017). Whether or not such interactions of density-dependent effects and abiotic conditions explain variation in the vital rates of plants and contribute to community dynamics still remains an open question, especially in temperate forests, despite considerable research efforts devoted to this field (McCarthy-Neumann & Ibañez, 2013; Brown et al., 2020; Yao et al., 2020).

Moreover, plants may be affected by density-dependent effects and local abiotic conditions differentially as their defences to natural enemies and tolerance to unfavourable habitat conditions and neighbouring individuals vary and may be stronger in taller plants (Barton & Koricheva, 2010; Piao et al., 2013; Yao et al., 2020). The growth form of plants may also play a role, as exemplified by the possibility that tree and shrub species differ in their ability to regenerate after enemy attack or episodic disturbance (Bellingham & Sparrow, 2000; Wang et al., 2020). Further, sensitivity to density-dependent effects and abiotic habitat conditions likely varies among species based on their life history strategies (Uriarte et al., 2018; Brown et al., 2020). For instance, sensitivity to negative density-dependent effects has been shown to increase with the species' shade intolerance (McCarthy-Neumann & Ibañez, 2013; Brown et al., 2020).

As density-dependent effects have been traditionally studied using a fixed neighbourhood size to capture the interactions between seedlings and their neighbours (Comita et al., 2009; Bai et al., 2012; Johnson et al., 2017), such an approach does, in our opinion, not fully account for the fact that the processes underlying these interactions

may operate at different spatial scales (Zambrano et al., 2019; Zambrano et al., 2020). For instance, the spatial scale of neighbourhoods over which seedlings experience density-dependent effects may differ among species (Queenborough et al., 2007), and likely also among plants of different sizes and growth forms. If density-dependent effects arise from competitive interactions, infection by fungal pathogens or herbivore foraging behaviour, it is unlikely that all these processes are equally important for all plants and species in a community (Hantsch et al., 2014; Champagne et al., 2016; Adler et al., 2018), or that they are reflected in the demography of these species by similar spatial patterns (Law et al., 2009; Hart et al., 2017). Therefore, we adopted a spatially explicit approach, allowing for the evaluation of density-dependent effects across a continuous range of spatial scales (Raventós et al., 2010; Wiegand & Moloney, 2014). We also used statistical neighbourhood models with variable neighbourhood size (Zambrano et al., 2020) to assess density-dependent effects (Piao et al., 2013; Johnson et al., 2014; Brown et al., 2020).

The focus of our study is on woody seedling mortality in an alluvial temperate forest. Although floods are typical of this forest type, their spatial extent, frequency and duration have largely been reduced after the regulation of large rivers, bringing about a gradual change towards species interactions and habitat differentiation driven by other factors than flooding disturbance (Ward & Stanford, 1995; Janík et al., 2011; Janík et al., 2016). In Europe, consequences of this change are that characteristic tree species of alluvial hardwood forests such as *Quercus robur* and *Fraxinus angustifolia* often fail to recruit, whereas flood-intolerant *Carpinus betulus* and *Acer campestre* are rapidly expanding (Trémolières et al., 1998; Glenz et al., 2006; Terwei et al., 2013; Janík et al., 2016). In this situation, local density-dependent effects and light gradient partitioning may play a more prominent role as drivers of species coexistence than the former broad-scale effect of flooding disturbance (Terwei et al., 2013; Janík et al., 2016).

Our main aim is to examine the relative importance of density-dependent effects and light availability as determinants of seedling mortality across multiple woody species, two seedling size classes (small and tall seedlings) and two growth forms (tree and shrub seedlings) in a rarely studied system: old-growth alluvial temperate forest. We specifically relate two-year seedling mortality to (a) density-dependent effects, (b) light availability, and (c) interactions between density-dependent effects and light availability. Three predictions of the relative importance of density-dependent effects and light availability were evaluated: density-dependent effects and light availability are more important: (a) for the mortality of small seedlings than for tall seedlings; (b) for the mortality of tree seedlings than for shrub seedlings; and (c) for seedling mortality of some species than others.

2 | METHODS

2.1 | Study site

The study was carried out in the Ranšpurk forest reserve (48°40' N, 16°56' E), which is part of a vast complex of lowland alluvial forests



in the southeastern region of the Czech Republic on the border with Austria and Slovakia. This naturally regenerated forest represents a unique old-growth forest remnant protected since 1949, with a total area of 22.25 ha. Intentional felling has not been recorded after 1873 and deadwood extraction has not been recorded after the 1930s (Vrška, 2006). Two flooding events have reached the area after 1990, in 1999 and 2005 (Vrška, 2006; Janík et al., 2016). The interannual mean \pm standard deviation for the 2000–2019 period was $10.8 \pm 0.6^\circ\text{C}$ for temperature and 496 ± 87 mm for precipitation. Approximately 60% of the annual precipitation falls during May–September (Czech Hydrometeorological Institute, <http://www.chmi.cz/>). The elevation ranges from 153 m to 156 m. The whole area is an alluvial floodplain, with undulating sand dunes rising 0.5–3 m above the surrounding area. The geological basement comprises recent Holocene sandy and clay-loamy sediments on fluvial gravels. Soils can usually be classified as Humic and Eutric Endogleyic Fluvisols and Humic and Eutric Epigleyic Fluvisols, with rare occurrences of Haplic Arenosols on sandy materials (Michéli et al., 2006). The tree canopy layer is mainly dominated or co-dominated by *Quercus robur* and *Fraxinus angustifolia* (*Fraxinus*), with an upper understorey of *Carpinus betulus* (*Carpinus*), *Acer campestre* (*Acer*), *Tilia cordata* and *Ulmus laevis*, and shrub species *Crataegus laevigata* (*Crataegus*), *Euonymus europaeus*, *Sambucus nigra*, *Pyrus pyrausta* and *Prunus* spp. in the lower understorey.

2.2 | Data collection

A regular grid with 21 square seedling plots (5 m \times 5 m), spaced 44.25 m apart, was established in 2016. The entire grid is included in a larger plot, established as a permanent research infrastructure in the study area. In this larger plot, all individuals ≥ 1 cm diameter at breast height (DBH) were tagged, mapped, measured for DBH and identified. In seedling plots, all seedlings of woody species (defined as ≥ 10 cm tall and ≤ 1 cm DBH) were mapped, tagged, identified and measured for height. In total, 1,232 seedlings and 18,158 trees were recorded. Seedling plots were re-censused in 2017 and 2018. In order to record seedling size in a way that is comparable among species, seedlings were classified as small and tall if their height was below and above species-specific means, respectively (Appendix S1, Table S1). Preliminary analyses showed that use of the median species-specific height as size threshold gave the same result and the former approach was therefore used.

2.3 | Statistical neighbourhood models

We analysed the probability of seedling mortality using generalised linear mixed models (GLMM) with a binomial error distribution and logit link as a function of variables used to characterise the response of focal seedlings to seedling and tree neighbours (density-dependent effects), light availability and elevation, and the interactions of density-dependent effects and light availability. Seedling mortality

was examined over the two-year census period (2016–2018). We calculated the density of conspecific, heterospecific and all seedling neighbours around each focal seedling (Appendix S1 Table S2). Seedlings within the 0.5-m radius of a focal seedling were considered seedling neighbours. To eliminate boundary effects, seedlings within 0.5 m of the seedling plot edge were excluded from the set of focal seedlings (Bai et al., 2012). We used the sum of basal areas of trees within the 5-, 10- and 15-m radius of each focal seedling to examine the effect of the density of neighbouring trees on seedling mortality.

Seedling mortality was modelled separately for each of ten data subsets to capture variation in seedling mortalities: (1) all seedlings (all species pooled), (2) small seedlings, (3) tall seedlings, (4) tree seedlings (five species), (5) shrub seedlings (five species), (6) seedlings of all species except *Acer campestre*, and (7–10) species-level models for the four species with ≥ 40 seedlings and ≥ 100 trees (three tree species *Acer*, *Carpinus*, *Fraxinus* and one shrub species, *Crataegus*; Appendix S1 Table S4). Data subsets (2) and (3) were obtained by splitting the full data set by seedling size, subsets (4) and (5) by splitting by growth form. Subset (6) was included to examine if an effect of the most abundant species in the seedling community, *Acer*, on seedlings of other woody species could be detected (Piao et al., 2013).

Because plants may differ in the strength and spatial scale of density-dependent effects (Zambrano et al., 2019; Zambrano et al., 2020), we used nine competing models, obtained for all combinations of three neighbourhood sizes (5-, 10- and 15-m radius) and three types of tree neighbours (conspecific, heterospecific and all), to select a neighbourhood size for each type of tree neighbour (Appendix S2 Figures S1–S2). In addition, we obtained three models with all tree neighbours (Appendix S2 Figures S3–S4). One set of twelve models, in which seedling mortality was related to just seedling height and density-dependent effects, was obtained for each of the 10 analysed data subsets (Appendix S1 Table S4). Within each set of nine or three models for each of the 10 data subsets, one model was selected by generating 1,000 bootstrap replicates of each data subset and refitting models with different combinations of neighbourhood sizes to each bootstrap replicate (Efron & Tibshirani, 1993). The model with the highest number of bootstrap replicates with the lowest Akaike's Information Criterion was selected (Appendix S2 Figures S1–S4; Burnham & Anderson, 2002).

To characterise the effects of abiotic habitat conditions we accounted for elevation while testing for the effects of canopy openness as a proxy for understorey light availability (Appendix S1 Table S2). Possible variation among tree species with respect to tolerance to flooding (Glenz et al., 2006), with flood-intolerant species preferring higher elevations (Janík et al., 2011), was accounted for by use of elevation as a proxy for position along a flooding gradient. As the frequency of flooding events has been strongly reduced at our site (Vrška, 2006), we include elevation in our models mainly due to the potential legacy effects of former flooding events on seedling distribution and demography. Furthermore, we took hemispherical photographs in the centre of each seedling plot under homogenous sky conditions at a height of 1.3 m with a Nikon D70 digital camera



mounted horizontally on a tripod with a Sigma 4.5 mm F2.8 EX DC fisheye lens. Photographs were analysed to estimate canopy openness using the WinSCANOPY software (Guay & Déry, 2017). Canopy openness, which varied from 5.25% to 19.09% at our site (median = 7.92%, Appendix S1 Table S2), was used to represent the understorey gap gradient of light availability (Lin et al., 2014; Wulantuya et al., 2020). Variations in light conditions have previously been shown to be an important driver of seedling vital rates (Comita et al., 2009; Lin et al., 2014; Jiang et al., 2020; Yao et al., 2020).

All continuous explanatory variables were standardised by subtracting the mean value of the variable and dividing by one standard deviation. Owing to large interspecific variation in seedling heights and the densities of conspecific, heterospecific and all seedling and tree neighbours, we standardised these variables within species (Fortunel et al., 2018). Species identity was included as a random intercept in the models with all species pooled to account for variation among species in the probability of seedling mortality. Since seedling mortality was likely to be spatially correlated, we also included seedling plot as a random intercept. We compared eight candidate models as follows: (1) a null model, (2) a density-independent model, (3) a non-specific density-dependent model, (4) a specific density-dependent model, (5) a habitat model, (6) a full model, (7) an interactive model with conspecific neighbours, and (8) an interactive model with conspecific and heterospecific neighbours. The last two

models included the interactions of light availability and density-dependent effects (Appendix S1 Table S3). The best-fit model was selected using the same procedure as in the case of models with variable neighbourhood sizes (Appendix S2 Figures S1–S4), but eight candidate models with the final neighbourhood sizes were refitted to each bootstrap replicate instead (Appendix S2 Figures S5–S6). Model parameters were considered statistically significant when 95% percentile confidence intervals based on 1,000 bootstrap replicates did not overlap zero (Bates et al., 2015). As the interaction of density-dependent effects and light availability was included in some best-fit models, the direct effects of seedling and tree neighbours on seedling mortality were only interpretable for mean light availability (Figures 1 and 2, Appendix S2 Figure S5, S6). All neighbourhood analyses were carried out in R 4.0.2 (R Core Team, 2020) using the library *lme4* 1.1-23 (Bates et al., 2015).

2.4 | Spatial point pattern analyses

We analysed the spatial pattern of seedlings with qualitative marks to examine if seedling mortality was influenced by seedling neighbours (the random labelling hypothesis; Illian et al., 2008). A qualitative mark (surviving/dead) was used to represent the seedling status in 2018, at the end of the census period. We used the mark

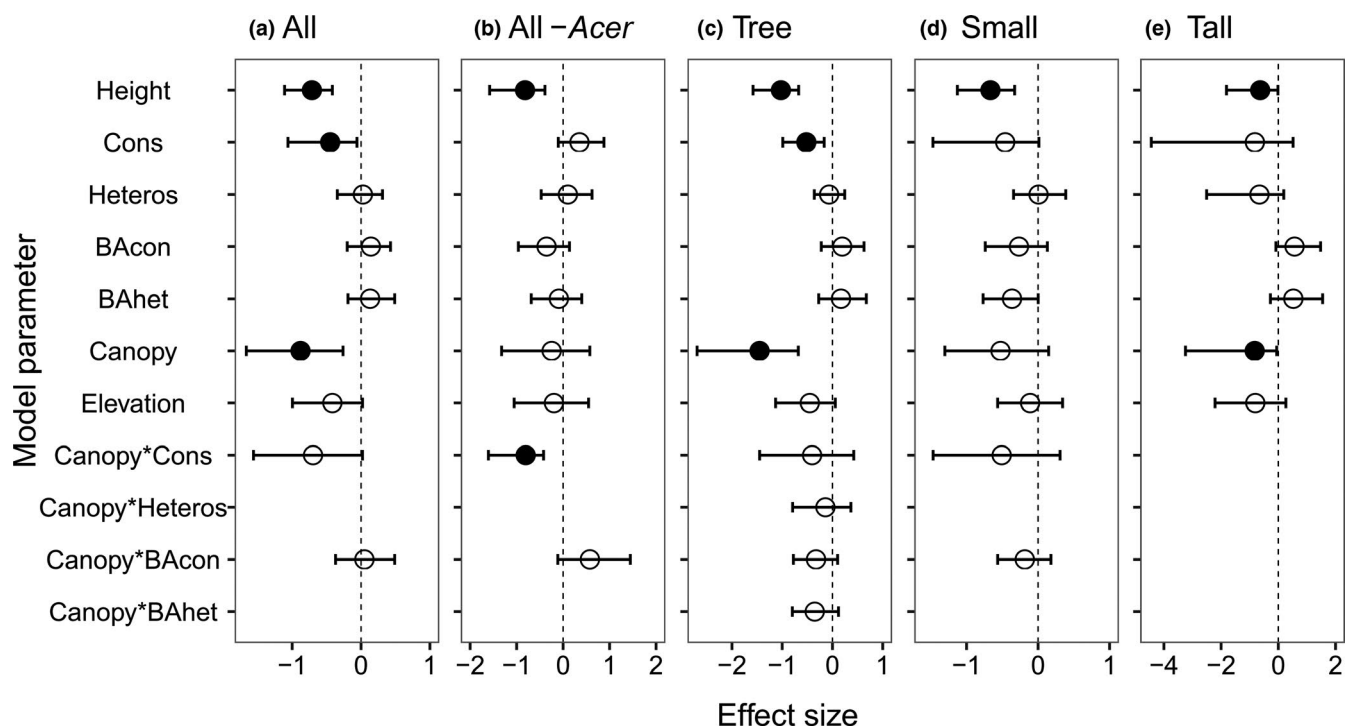


FIGURE 1 Effect sizes of standardised regression coefficients related to the mortality of (a) all seedlings, (b) woody seedlings other than *Acer*, (c) tree, (d) small, and (e) tall seedlings. Solid symbols denote significant effect sizes. Horizontal error bars indicate 95% percentile confidence intervals based on 1,000 bootstrap replicates. Only effect sizes of the best-fit candidate models are displayed. Abbreviations of parameters: Height (initial seedling height), Cons (density of conspecific seedlings), Heteros (density of heterospecific seedlings), BAcon (basal area of conspecific trees), BAhet (basal area of heterospecific trees), Canopy (canopy openness), and Elevation. An asterisk denotes the interaction of light availability (canopy openness) and density-dependent effects (the density of seedling and tree neighbours). The interactions with effect sizes below/above zero suggest negative/positive density-dependent effects at low light levels

connection function based on the classical pair correlation function (Wiegand & Moloney, 2014). The univariate variant of pair correlation function $g(r)$ can be defined as the expected number of points at distance r from a typical point of the pattern relative to the intensity λ of the pattern (Wiegand & Moloney, 2014).

Let 1 be the subscript of a “dead” seedling mark, 2 of a “surviving” seedling mark, and let h indicate the identity of a heterospecific seedling neighbour. To characterise the probability of focal seedling mortality as a function of distance to seedling neighbours, we used two variants of the mark connection function $p_{a,1}(r)$ in which seedling neighbours a were separately represented by conspecific $1 + 2(p_{1+2,1})$ and heterospecific h seedlings ($p_{h,1}$). In the general form, these test statistics were calculated as follows:

$$p_{a,1}(r) = \frac{\lambda_1}{(\lambda_1 + \lambda_2)} \times \frac{g_{a,1}(r)}{g_{a,1+2}(r)} \quad (1)$$

where $(\lambda_1 + \lambda_2)$ and λ_1 are the intensities of seedlings of the focal species and of dead seedlings of the focal species, respectively and g represents specific bivariate pair correlation functions (Wiegand & Moloney, 2014). A higher and lower probability of seedling mortality in the proximity of seedling neighbours is expected when $p_{a,1}(r) > \lambda_1/(\lambda_1 + \lambda_2)$ and $p_{a,1}(r) < \lambda_1/(\lambda_1 + \lambda_2)$, respectively (Raventós et al., 2010). These test statistics were only used to assess density-dependent effects at the species level, because we did not have enough data to ensure correct randomisation procedures of seedling marks in other data subsets (Velázquez et al., 2016).

We examined the density-dependent mortality of seedlings up to a distance of 2.5 m. To assess whether the observed patterns deviated from the null model, we carried out 999 Monte Carlo simulations of the random labelling null model and chose the 25th lowest

and 25th highest values at a given scale r to represent 95% simulation envelopes (Raventós et al., 2010; Wiegand & Moloney, 2014). We used the method of replicated patterns to obtain the average response of a given test statistic. In each case, seedling plot acted as a replicate pattern; however, we selected only plots with more than 10 seedlings on at least four seedling plots to be pooled into a single aggregate function (Illian et al., 2008). This restricted the species-level analyses to three tree species (*Acer*, *Carpinus*, *Fraxinus*) and one shrub species (*Crataegus*). All spatial point pattern analyses were conducted in the Programita software version 2018 (Wiegand & Moloney, 2014).

3 | RESULTS

3.1 | Scaling of density-dependent effects

The results of neighbourhood models showed considerable variation in the spatial extent of interactions with tree neighbours, depending on size class, growth form and species of focal seedlings. Heterospecific tree neighbours influenced seedling mortality within a 15-m radius, except for the mortality of small seedlings which was influenced within a 10-m radius (Appendix S2 Figure S1). The mortality of all seedlings was influenced by conspecific tree neighbours within a 5-m radius, the mortality of small and tall seedlings within a 10-m radius, and the mortality of tree seedlings within a 15-m radius (Appendix S2 Figure S1). Seedling mortality of individual species was similarly influenced by conspecific tree neighbours within different distances (Appendix S2 Figure S2). The mortality of shrub and *Crataegus* seedlings was most strongly influenced by all tree neighbours within 15- and 10-m radii, respectively (Appendix S2 Figures S3–S4).

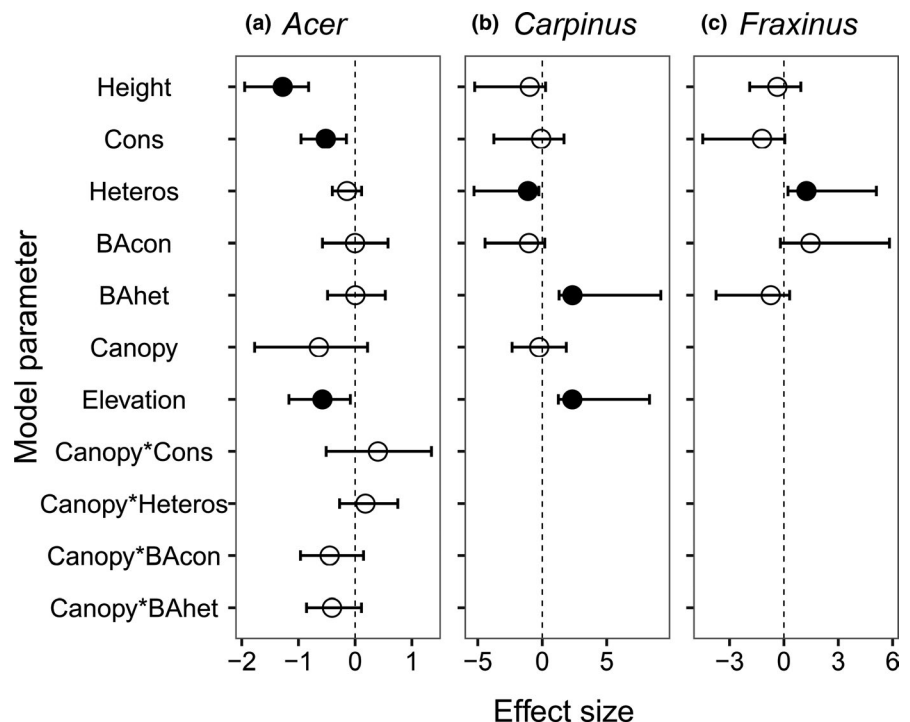


FIGURE 2 Effect sizes of standardised regression coefficients related to the mortality of (a) *Acer*, (b) *Carpinus* and (c) *Fraxinus* seedlings. For other conventions, see Figure 1



Neighbourhood models also showed that seedlings responded to seedling neighbours within a 0.5-m radius (Figures 1–3). However, the results of spatial analyses indicated that these density-dependent effects were detectable also at larger distances, up to 2.5 m from seedling neighbours. While *Acer* seedlings experienced spatially extensive density-dependent effects of seedling neighbours, seedlings of other species were exposed to spatially limited density-dependent effects (Figure 4).

3.2 | Direct density-dependent effects

Seedling and tree neighbours had a direct effect on seedling mortality (Appendix S2 Figures S5–S6). The results of neighbourhood models showed that the direct effects of conspecific

seedling neighbours (i.e. irrespective of the interactions with light availability) on the performance of all seedlings were positive (Figure 1a). Conspecific positive density-dependent effects were similarly observed in tree (Figure 1c), small (Figure 1d), *Acer* (Figure 2a), and *Fraxinus* seedlings (Figure 2c). Moreover, heterospecific seedling neighbours were associated with reduced mortality of *Carpinus* seedlings (Figures 2b and 4c) and increased mortality of *Fraxinus* seedlings (Figure 2c). In addition, a negative effect of all seedling neighbours on *Crataegus* seedlings was observed (Figure 3b), whereas the mortality of shrub seedlings was density-independent (Figure 3a). The results of spatial analyses showed weak density-dependent effects on individual species (Figure 4), corresponding to the direct effects of seedling neighbours in neighbourhood models (Figure 2).

The direct effects of conspecific and heterospecific tree neighbours were not significant and did not differ among seedlings of different growth forms and species, except for increasing mortality of *Carpinus* seedlings associated with heterospecific tree neighbours (Figure 2b). However, tree neighbours were associated with a tendency for reduced mortality of small seedlings, whereas the opposite was true for tall seedlings (Figure 1d,e).

3.3 | Direct effects of light availability and elevation

Light availability and elevation had direct effects on seedling mortality, except for shrub and *Fraxinus* seedlings (Figures 1–3, Appendix S2 Figures S5–S6). All seedlings, tree seedlings and tall seedlings experienced higher mortality at low light levels (Figure 1a,c,e). We also found significantly higher mortality of *Acer* and *Carpinus* seedlings at lower and higher elevations, respectively (Figure 2a,b).

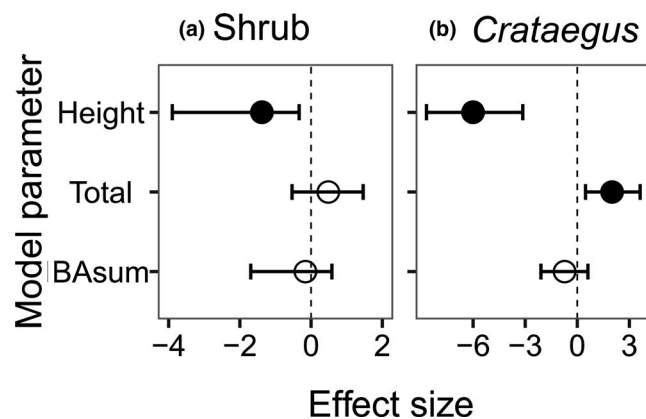


FIGURE 3 Effect sizes of standardised regression coefficients related to the mortality of (a) shrub and (b) *Crataegus* seedlings. Abbreviations of parameters: Height (initial seedling height), Total (total density of seedlings) and BAsum (total basal area of trees). For other conventions, see Figure 1

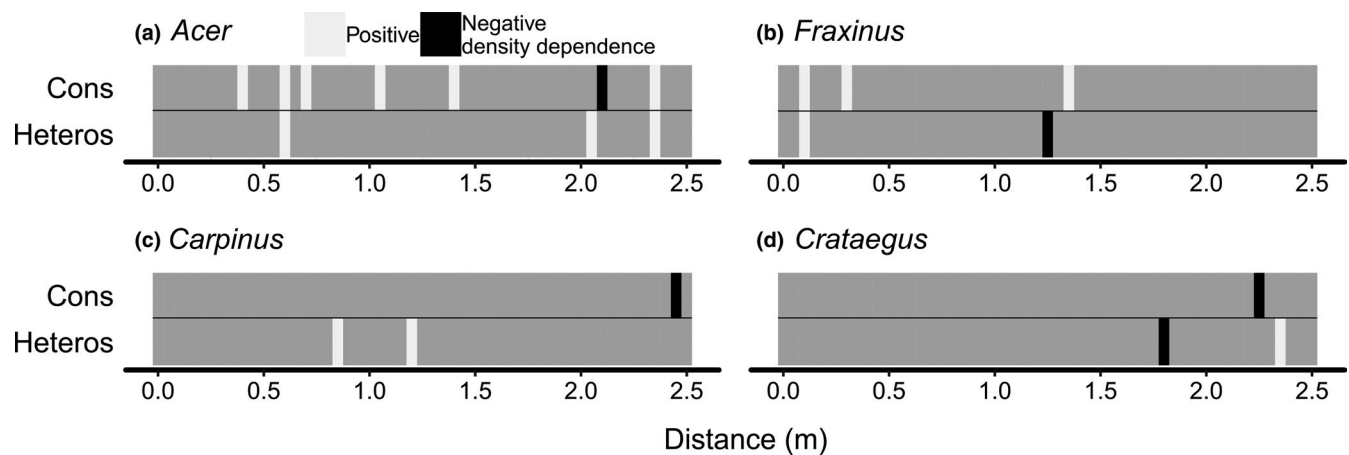


FIGURE 4 Trivariate random labelling analyses. The $p_{1+2,1}$ and $p_{h,1}$ mark connection functions were used as test statistics to examine the probability of seedling mortality as a function of the distance to conspecific and heterospecific seedlings with random labelling as a null model. The analyses were carried out at the level of individual species (a–d) to detect conspecific (Cons) and heterospecific (Heteros) density-dependent mortality and are displayed as lines in each respective subplot. The grey colour denotes no departure from random mortality. Significant departures were constructed through 999 Monte Carlo simulations of the null model with the 25th largest and 25th smallest values representing 95% simulation envelopes



3.4 | The interactions of density-dependent effects and light availability

A significant interaction between neighbour density and light availability was found in all models of seedling mortality except the models for tall, *Crataegus* and *Fraxinus* seedlings (Figures 1–3, Appendix S2 Figures S5–S6). While a significant interaction between conspecific neighbours and light availability was found in the set of all seedlings and small seedlings (Figure 1a,d), significant interactions both with conspecific and heterospecific neighbours were found for tree and *Acer* seedlings (Figures 1c and 2a, Appendix S2 Figures S5–S6).

The mortality of all seedlings tended to increase with more conspecific seedling neighbours at low light levels (Figures 1a and 5a), while no relationship with the interaction of conspecific tree neighbours and light availability was found (Figure 1a). Tendencies for a relationship between some interactive effects and an increase in the mortality of tree and small seedlings were found at low light levels (Figure 1c,d). Moreover, the mortality of woody seedlings other than *Acer* increased significantly with more conspecific seedling neighbours at low light levels (Figures 1b and 5b).

4 | DISCUSSION

4.1 | Scaling of density-dependent effects

Our results illustrate that woody seedlings may respond to both seedling and tree neighbours at different spatial scales, depending on the size class, growth form and species of the seedlings. This is consistent with current views that processes operating at plant neighbourhood scales play a fundamental role in structuring plant

communities (Adler et al., 2018) and, accordingly, the size of plant neighbourhoods as well as the identity of plant neighbours are essential for understanding how plant performance is influenced by species interactions (Zambrano et al., 2020).

We cannot, however, account for the causes of this scale dependence in our study because the zone of influence of seedling and tree neighbours on seedling mortality is likely to result from species-specific processes and life histories (Lasky et al., 2015; Detto et al., 2019; Zambrano et al., 2019; Zambrano et al., 2020). Seedling response to conspecific tree neighbours may be an outcome of multiple and often highly complex processes, such as pressure from different loads of host-specific enemies (Liang et al., 2016; Liu & He, 2019), intraspecific interactions (Adler et al., 2018) and mycorrhizal infections (Waud et al., 2016; Wulantuya et al., 2020), likely operating at scales both within and beyond seedling neighbourhoods. Depending on the spatial scale of neighbourhoods (Zambrano et al., 2020), seedling performance may also be reduced by functionally similar and/or dissimilar tree neighbours as a result of habitat filtering and/or niche differentiation processes, respectively (Lasky et al., 2015; Chen et al., 2016). The role of functional similarity was not examined in our study.

Moreover, our findings suggest that the size of heterospecific neighbourhoods over which trees influence seedling mortality is less spatially variable than the size of conspecific neighbourhoods, with heterospecific trees influencing seedling mortality mostly within the distance of 15 m. Pathogens with broad host ranges (Hersh et al., 2012) or density-responsive generalist vertebrate herbivores, i.e. that are not strongly selective for any particular plant species (Manson et al., 1998; Wulantuya et al., 2020), may potentially account for this spatially consistent seedling response to heterospecific tree neighbours. It is also possible that the spatial scales at which interspecific interactions between trees and seedlings take place are more similar

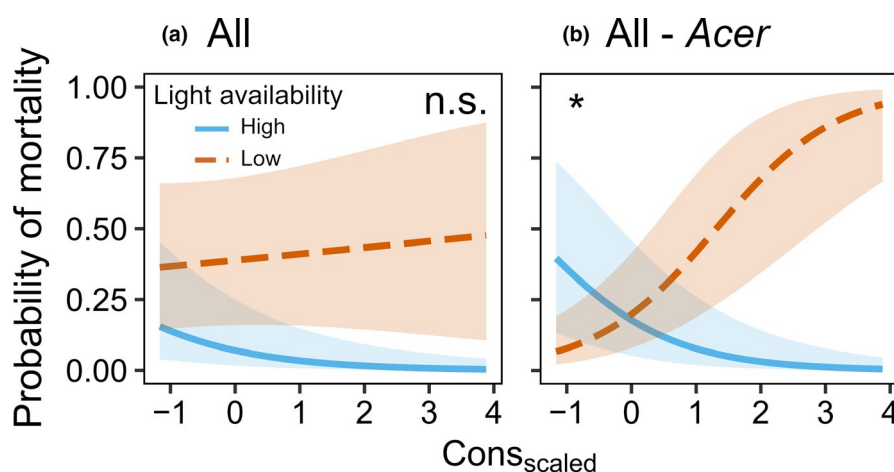


FIGURE 5 The interactive effects of conspecific seedling density ($\text{Cons}_{\text{scaled}}$) and light availability (canopy openness) on the mortality of (a) all seedlings and (b) seedlings other than *Acer*. Low and high light availability are represented by the 5% and 95% quantiles of canopy openness, respectively. The best-fit candidate models (Figure 1) were used to calculate the predicted probabilities and 95% confidence intervals. The interaction was not significant in panel (a) with $p > 0.05$ (n.s.) and significant in panel (b) with $p < 0.001$ (*). Conspecific seedling density was standardised within species ($\text{Cons}_{\text{scaled}}$) by subtracting the species-specific mean of conspecific seedling density and dividing by one species-specific standard deviation



than the scales of intraspecific interactions, because the prevailing effect of heterospecific tree neighbours on seedling mortality may result mostly from the interactions with a single or only few abundant tree species, such as *Acer* or *Carpinus* at our site.

In addition to the results of our neighbourhood models, we also detected species-specific seedling responses to seedling neighbours using spatial point pattern analyses. Even though these species-specific signs of density-dependent effects were generally weak compared to the results of neighbourhood models using a fixed 0.5-m neighbourhood radius, they were detected at various distances up to 2.5 m from seedling neighbours. Our findings thus indicate that the spatial distribution of seedlings carries a spatial signature (i.e. spatial correlation between dead seedlings and seedling neighbours) related to interspecific variation in density-dependent effects (Velázquez et al., 2016). Moreover, we find the result that seedling mortality was influenced by seedling neighbours even beyond 0.5 m important. This suggests that the estimation of density-dependent effects may be biased when using a single spatial definition of plant neighbourhoods (Zambrano et al., 2019; Zambrano et al., 2020). The full range of density-dependent effects may also go undetected when an inappropriate spatial scale is selected (Velázquez et al., 2016; Detto et al., 2019). This may be problematic especially for rare species with relatively low conspecific densities, at which some types of density-dependent effects may still occur. Such density-dependent effects can be exemplified by some vertebrate herbivores that are known to be more selective for less palatable plants growing nearby more palatable heterospecific plants (i.e. associational susceptibility; Bee et al., 2009). On the other hand, unpalatable heterospecific seedlings may reduce herbivory damage on palatable seedlings (i.e. associational resistance; Barbosa et al., 2009; Champagne et al., 2016). Other density-dependent mechanisms such as intraspecific competition for resources and the pressure from soil-/airborne fungal pathogens are also likely to contribute to establishment of an upper spatial scale for seedling neighbourhoods (Queenborough et al., 2007; Germany et al., 2019), resulting from seedling size variation in resource acquisition (Berntson & Wayne, 2000) or pathogen capacities to spread (Hantsch et al., 2014; Liu & He, 2019), respectively. Moreover, resource transfer via mycorrhizal connections of seedling roots may also drive seedling performance depending on the density and distance between seedlings (Nara, 2006; Teste et al., 2009; Waud et al., 2016).

4.2 | Density-dependent effects vary with light availability

Our findings from an alluvial temperate forest suggest that the direction of density-dependent effects on seedling mortality may be related to variation in light availability, as plants may respond differentially to their neighbours in favourable and less favourable habitats (Zambrano et al., 2017; Uriarte et al., 2018).

Specifically, we find negative density-dependent effects (conspecific inhibition) on the survival of woody seedlings other than

Acer under low-light conditions (McCarthy-Neumann & Ibañez, 2013). This result supports the view that conspecific inhibition at low light levels is mediated by intraspecific competition (Chesson, 2000; Adler et al., 2018) and/or host-specific enemies such as soil pathogens associated with high conspecific densities (McCarthy-Neumann & Ibañez, 2013; Pfennigwerth et al., 2018; Jiang et al., 2020). Under these conditions, host-specific pathogens are expected to benefit from either increased virulence or the susceptibility of host plants, as the costs of plant defence are usually higher (Roberts & Paul, 2006). Intraspecific competition among seedlings for water may also be stronger at low light levels because plants invest more resources in aboveground biomass under these conditions, thus increasing the transpiration surface and susceptibility to desiccation (Holmgren et al., 1997). Alternatively, the failure of seedlings to compensate for the carbon demand of their mycorrhizal symbionts may potentially increase conspecific inhibition under low-light conditions (Allsopp & Stock, 1992; Konvalinková & Jansa, 2016; Jiang et al., 2020).

4.3 | Variation in seedling response among size classes

We find that the effects of density dependence and light availability on seedling mortality depend on seedling size variation. The role of seedling size is, however, more complex than originally expected, indicating that small seedlings experience conspecific inhibition related to low-light conditions, in line with the assumption that intraspecific competition and/or host-specific enemies induce density-dependent mortality in unfavourable habitat conditions (Liu & He, 2019; Jiang et al., 2020; Wulantuya et al., 2020). Tall seedlings are probably more resistant to conspecific inhibition than small seedlings in our study, perhaps because tall seedlings can divert more resources to tissue defence (Develey-Riviere & Galiana, 2007; Barton & Koricheva, 2010) or attain greater carbon gains from neighbouring trees than small seedlings (Teste et al., 2009). However, we cannot rule out the possibility that the growth rather than the survival of tall seedlings is reduced by conspecific inhibition (Brown et al., 2020), especially over the relatively short two-year period of our study. In contrast to our initial expectations, the survival of tall seedlings appears to be inhibited by conspecific and heterospecific tree neighbours, suggesting that size-asymmetric competition with trees and/or density-responsive generalist enemies becomes important once seedlings are taller (Dickie et al., 2005; Kupferschmid et al., 2020; Wulantuya et al., 2020). As the survival of tall seedlings is also reduced under low-light conditions irrespective of tree neighbours, our findings support variation in density-dependent effects and abiotic niche partitioning across plant life stages (Lasky et al., 2015; Zambrano et al., 2019; Yao et al., 2020). Specifically, conspecific inhibition of plant survival is often stronger at early life stages, while abiotic habitat conditions become more important at later life stages (Bai et al., 2012; Yao et al., 2020). However, we also show that asymmetric competition with trees may be important for taller seedlings.



4.4 | Variation in seedling response among growth forms and species

In accordance with our second and third predictions, the responses of seedlings to neighbour density and light availability are determined by growth form and species identity. More specifically, generalist enemies or competition with neighbours may drive the mortality of tree seedlings when less light is available, as tree seedlings respond to the interaction with both tree and seedling neighbours, irrespective if they are conspecific or heterospecific. Although this is consistent with the fact that plant performance usually decreases in unfavourable habitats with more neighbours (Zambrano et al., 2017), we find lower reduction with more conspecific seedling neighbours, perhaps mediated by a positive effect of mycorrhizal infection (Nara, 2006; Teste et al., 2009; Crawford et al., 2019). In this scenario, net soil feedbacks are expected to be less negative for seedlings with many conspecific seedling neighbours than with heterospecific neighbours at low light levels, because it is more likely that seedlings with conspecific neighbours will benefit more from an association with the same mycorrhizal fungi compared to seedlings with heterospecific neighbours having both the same and different types of mycorrhizas (Crawford et al., 2019; but see Montesinos-Navarro et al., 2019). This benefit may result from sharing different resources or defence signals via a common mycorrhizal mycelium connecting the root systems of conspecific seedlings (Teste et al., 2009; Simard et al., 2012).

However, this clearly deserves future investigations at our site because species associated with arbuscular mycorrhizae usually exhibit strong conspecific inhibition near conspecific individuals (Bennett et al., 2017; Crawford et al., 2019; Brown et al., 2020; Jiang et al., 2020), while they may benefit near heterospecific individuals with different mycorrhizal types (Wulantuya et al., 2020). This strong conspecific inhibition may, in particular, apply to *Fraxinus* and *Acer* seedlings which are associated with arbuscular mycorrhizae (Wang & Qiu, 2006). Conversely, *Carpinus* and *Tilia cordata* seedlings are ectomycorrhizal (Wang & Qiu, 2006) and may therefore experience weaker conspecific inhibition due to better protection against pathogens (Bennett et al., 2017; Brown et al., 2020; Jiang et al., 2020). In contrast to these expectations, we show that heterospecific rather than conspecific neighbours reduce the performance of *Carpinus* and *Fraxinus* seedlings, suggesting that some negative interspecific interactions may not indicate a stable coexistence among species (Broekman et al., 2019). Such stronger interspecific interactions may be expected when colonisation by new or formerly rare species follows an environmental perturbation (Urban et al., 2012). This situation may correspond to the expansion of *Carpinus* and especially *Acer* after the reduction of the magnitude and frequency of flooding events at our site (Vrška, 2006; Janík et al., 2016). As we find no evidence for conspecific or heterospecific inhibition of *Acer* seedlings, *Acer* may possibly outperform seedlings of other species in the partitioning of currently flood-free habitats (Trémolières et al., 1998; Janík et al., 2011; Janík et al., 2016), perhaps due to a stress-tolerant ruderal strategy (Brzeziecki & Kienast, 1994). It is also possible

that *Acer*, as the most abundant species, is responsible for the weaker density-dependent effects observed for the seedling community as a whole (Piao et al., 2013), because the performance of woody seedlings other than *Acer* is clearly affected by conspecific inhibition from seedling neighbours at low light levels. Given that regular floods are absent and the vertical forest structure follows the current trend of gap-filling (Janík et al., 2011), we also suggest that heterospecific inhibition of relatively light-demanding and flood-tolerant *Fraxinus* seedlings may indicate a recent stagnation of *Fraxinus* population (Janík et al., 2016). Even though we similarly find that heterospecific trees reduce the survival of *Carpinus* seedlings, *Carpinus* is a relatively shade-tolerant species which may potentially outperform other species under dense closed-canopy conditions (Janík et al., 2011; Legner et al., 2014; Janík et al., 2016).

Moreover, we postulate vegetative resprouting as a possible explanation of the indifference of shrub seedlings to density- and light-dependent effects, potentially allowing shrubs to persist even under pressure from host-specific enemies, neighbouring individuals and/or unfavourable shade conditions (Bellingham & Sparrow, 2000). However, seedlings of *Crataegus*, the shrub species with the highest seedling abundance, responded negatively to high densities of seedling neighbours. Our own observations indicate that *Crataegus* seedlings are extensively damaged by ungulate herbivores and, accordingly, that resprouting or other antiherbivore strategies do not apply to a species which is extensively preferred by herbivores over others (Miller et al., 2007).

Finally, we illustrate that how density-dependent effects translate into demographic outcomes for woody seedling populations may be driven by variation in local understorey light levels. If negative density-dependent effects are truly restricted to unfavourable habitats such as those with low light levels, identifying the underlying processes (e.g. plant-soil biota interactions; Konvalinková & Jansa, 2016; Wulantuya et al., 2020) and spatial resolution of this habitat heterogeneity may in turn elucidate how important and extensive these processes are in structuring forest communities (Hart et al., 2017). From this point of view, our findings suggest that both seedling and tree neighbours may contribute to the strength and spatial variation in density-dependent effects at seedling neighbourhood scales, depending on the size class, growth form and species of woody seedlings. However, further examinations of how specific drivers of density-dependent effects relate to plant neighbourhood scales are needed, because our findings indicate that large spatial variation in density-dependent effects may result from complex species-specific processes and life histories.

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CONFLICT OF INTEREST

The authors have no conflicts of interest to declare.



AUTHOR CONTRIBUTIONS

JH, DJ and DA conceived and designed this study; JH conducted fieldwork, analysed the data and wrote the manuscript.

DATA AVAILABILITY STATEMENT

The data that support the findings of this study are available from the corresponding author upon request.

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SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section.

Appendix S1. Overview of model parameters, candidate neighbourhood models and data subsets.

Appendix S2. Model selection using variable neighbourhood size.

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