



Neighbourhood effects modify deer herbivory on tree seedlings

Jan Holík^{1,2} · David Janík¹ · Libor Hort¹ · Dušan Adam¹

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Abstract

As spatially fine-scale foraging decisions are intrinsic to browsing herbivores such as deer, the search and selection of individual plants may be shaped by the density of neighbouring plants. However, how such neighbourhood effects may modify herbivore foraging decisions at different spatial scales is largely unexplored. Our main goal was to examine deer foraging preferences for tree species and seedling sizes, and to ask whether the spatial relationship of unbrowsed and browsed seedlings was indicative of different neighbourhood effects at the spatial scale of seedling neighbourhoods. We used two data sets from an old-growth temperate forest: (1) a seedling inventory and (2) fully mapped transect data, and applied a generalized linear mixed model and spatial point pattern analyses, respectively. We found that neighbourhood effects modified deer foraging behaviour depending on the proximity, density and species identity of neighbours, which, in turn, determined the strength and spatial extent of browsing impacts on tree seedlings. While sycamore maple seedlings experienced the highest levels of deer selectivity, deer were selective for European beech seedlings only within short distances. Beyond these distances, beech seedlings were browsed only opportunistically, as conspecific neighbours ceased to modify deer selectivity. Beech seedlings were also more susceptible to browsing within short distances from silver fir seedlings, indicating an associational susceptibility. As fir seedlings experienced strong and extensive density-dependent deer selectivity both near conspecific and beech neighbours, using such neighbourhood effects may not be a promising tool to prevent deer browsing on tree seedlings at the spatial scale of seedling neighbourhoods.

Keywords Deer browsing · Foraging behaviour · Seedling dynamics · Tree regeneration · Spatial point patterns · Deer diet preferences · Density-dependent effects · Plant–herbivore interactions · Associational effects · Deer herbivory · Old-growth forest

Introduction

The spatial distribution of food resources across a landscape and foraging behaviour is the main drivers of variation in the diet composition of ungulate herbivores (Beckerman and Oksanen 2005; Abbas et al. 2011; Massé and Côté 2012). Their foraging behaviour arise from decisions made at multiple spatial and temporal scales (Senft et al. 1987; Bailey

et al. 1996). At the largest spatial scales, abiotic constraints such as physical landscape properties may be important for the selection of preferred habitats (Bailey et al. 1996; Milchunas and Noy-Meir 2002), which typically form a discontinuous mosaic of vegetation patches within a landscape (Abbas et al. 2011; Jarnemo et al. 2014). As a result, ungulate herbivores often exhibit selective foraging, described as a hierarchy of decisions that herbivores make at various spatial scales in order to locate a preferred habitat and efficiently exploit food resources (Illius et al. 2002; Morellet et al. 2011).

Spatial variation in food availability and ungulate densities usually determine the spatial scale at which these herbivores are selective (Hjältén et al. 1993; Bee et al. 2009). For instance, ungulates may make foraging decisions at the spatial scales of larger vegetation patches such as forest stands (Hjältén et al. 1993), or at much finer scales corresponding to individual plants and plant aggregations (Danell

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✉ Jan Holík
xholik4@gmail.com

¹ Department of Forest Ecology, The Silva Tarouca Research Institute for Landscape and Ornamental Gardening, Brno, Czech Republic

² Department of Silviculture, Faculty of Forestry and Wood Technology, Mendel University in Brno, Brno, Czech Republic

et al. 1991; Miller et al. 2007). The former assumes that herbivores travel and select between patches (Arditi and Dacorogna 1988; Hjältén et al. 1993; Bergvall et al. 2006), with nutrient-rich sites being found through spatial memory (Fryxell et al. 2008; Gautestad et al. 2013) or visual cues, allowing herbivores to find and assess food sources from a distance (Zollner and Lima 1999). On the other hand, movements and feeding within patches assumes that food selection and individual host-finding take place through different visual and olfactory cues at the scales of plant neighbourhoods (Tsegai et al. 2013; Hämbäck et al. 2014; Kim and Underwood 2015), involving confrontations with plant traits related to anti-herbivore defence strategies (Pellissier 2013; Ohse et al. 2017a), palatability and nutritional value (Alm et al. 2002; Storms et al. 2008; Abbas et al. 2011).

Recent findings on the foraging behaviour of browsing herbivores, such as red deer (*Cervus elaphus* L.) and roe deer (*Capreolus capreolus* L.), have shown that it is determined not only by the quality (i.e. species palatability), but also by the quantity (i.e. frequency and density) of focal and non-target neighbouring plant species (Bee et al. 2009; Milligan and Koricheva 2013; Bobrowski et al. 2015), underscoring the role of frequency- and density-dependent neighbourhood effects in plant–herbivore interactions (Barbosa et al. 2009; Hämbäck et al. 2014). As an example of heterospecific neighbourhood effects, a high forage quality of heterospecific neighbouring plants (e.g. herbs and palatable woody species) often leads to frequent browsing of the species in question (i.e. associational susceptibility; Bergvall et al. 2006; Häslér and Senn 2012). The pressure from browsing may be, on the contrary, relieved when attractive species grow near less palatable heterospecific species (Hjältén et al. 1993; Bee et al. 2009) and species providing alternative forage (Baraza et al. 2006; Perea and Gil 2014) or mechanical barriers to browsing (Maltoni et al. 2019), corresponding to a situation when a species becomes more resistant to herbivory near a “repellent” species (i.e. associational resistance; Tahvanainen and Root 1972; Atsatt and O’Dowd 1976). These two types of associational effects are inherently frequency- or density-dependent, even though the outcomes of associational resistance and susceptibility are opposite, i.e. beneficial or detrimental to the focal plant (Barbosa et al. 2009; Hämbäck et al. 2014; Kim and Underwood 2015), respectively. Similarly, conspecific neighbourhood effects may arise when the probability of herbivory increase or decrease with conspecific seedling density, resulting in resource concentration and dilution effects (Root 1973; Otway et al. 2005; Kim and Underwood 2015), respectively. Ultimately, if a resource concentration effect inhibits plant performance (e.g. growth and survival), this conceptually coincides with so-called Janzen-Connell effects, predicting that specialized herbivores and other natural enemies control

the size of plant populations (Janzen 1970; Connell 1971; Forrister et al. 2019).

Although the concept of density and frequency dependence was appreciated already in early studies of neighbourhood effects on plant–herbivore interactions (Tahvanainen and Root 1972; Root 1973; Atsatt and O’Dowd 1976), there has long been missing an explicit recognition of spatial scales at which different types of neighbourhood effects arise (Barbosa et al. 2009; Underwood et al. 2014; Champagne et al. 2016). At larger spatial scales, herbivores may be substantially compromised in their search for host plants and reduced to between-patch foraging decisions owing to their limited sensory ability to evaluate individual plant qualities (Hjältén et al. 1993; Hämbäck et al. 2009). However, the situation may be rather different at much finer spatial scales such as the scales of plant neighbourhoods (i.e. the scales at which the focal plant can be directly or indirectly influenced by neighbouring plants), because the motivation and sensory ability of herbivores to select individual plants may depend both on the density and distance between plants (Hämbäck et al. 2009; Underwood et al. 2014). Even though the role of plant spatial arrangement (i.e. variation in distance between plants) has already been tested in various experimental settings (Bergman et al. 2005; Wang et al. 2010; Tsegai et al. 2013), we generally lack spatially explicit evidence on fine-scale herbivore foraging behaviour given the natural spatial distributions of plant species and variation in local plant density and distance between plants (but see Oom et al. 2002; Hämbäck et al. 2009 for ungulate and insect herbivory, respectively). This is fundamental, however, for understanding and managing these impacts of herbivory, e.g. on tree regeneration in production forests.

Moreover, the apparency of patches and individual plants plays a role in deer foraging decisions at different spatial scales (Reimoser and Gossow 1996; Kupferschmid et al. 2013). While individual plant size may not be as important as the overall patch size at larger spatial scales (Pietrzykowski et al. 2003; Miller et al. 2006), it is a fundamental criterion of deer foraging selectivity at smaller spatial scales. At these small scales, the strength of the relationship between seedling size and deer foraging selectivity likely depends on deer preferences for a particular tree species (Ammer 1996; Klopčič et al. 2010). If this relationship is particularly strong (Simončič et al. 2019; Kupferschmid et al. 2020), deer browsing may potentially have an important impact on the height structure of seedling populations even at the scales of seedling neighbourhoods.

As the main goal of this study, we examined whether deer browsing was selective for particular species and seedling sizes, and whether and how the spatial relationship of unbrowsed and browsed seedlings was indicative of different types of conspecific and heterospecific neighbourhood effects at the spatial scale of seedling neighbourhoods. In

addition to statistical models using seedling inventory data, we examined fully mapped seedling data using spatial point pattern analysis, as this may be particularly useful for the reconstruction of non-random processes such as herbivore foraging decisions and for the identification of spatial scales across which these processes operate (Wiegand and Moloney 2014). Importantly, we were not interested in the underlying spatial distribution of seedlings per se, but rather in spatial relationships (correlation structures) among different types of neighbouring seedlings (e.g. browsed and unbrowsed seedlings) conditional on the existing seedling locations. As these spatial relationships are characterized by the density (size) of neighbouring seedlings and the distance between them (Law et al. 2009), they may indicate whether deer browsing on tree seedlings is influenced by the seedling neighbourhood in which they are growing. We specifically addressed the following questions (Table 1): (1) How does the probability of a browsing event vary depending on the species, size classes and densities of seedlings, and are the effects of seedling density species-specific? (2) Do spatial relationships of browsed and unbrowsed seedlings indicate deer foraging preferences for particular species? (3) Do seedlings become resistant/susceptible to deer browsing depending on the proximity to conspecific and heterospecific seedlings? (4) Are seedling sizes spatially correlated with unbrowsed and browsed seedlings, indicating deer foraging preferences for certain sizes?

Methods

Study site

The study was carried out in the Salajka forest reserve in the Czech Republic (49° 24' N 18° 25' E), a representative remnant of mixed old-growth forests in the Western Carpathians. The dominant tree species are *Fagus sylvatica* L. (beech) and *Abies alba* Mill. (fir) amounting to 70 and 20% of the total tree basal area, respectively. *Picea abies* (L.) H. Karst. (spruce) and *Acer pseudoplatanus* L. (maple) are mostly rare. The mean annual temperature is 5.4 °C, and the mean annual precipitation is 1144 mm. The elevation ranges from 715 to 820 m. The maximal snow depth usually amounts to 1 m in winter. The area belongs geologically to the flysch zone of the Western Carpathians, with soils mostly classified as silt-loam, loam and clay-loam Haplic Cambisols (Michéli et al. 2006). The site, with a total area of 21.9 ha, has been unmanaged since 1937 and was legally designated a forest reserve in 1956. Based on game censuses from two nearby forest reserves, the average population densities of the deer species *C. elaphus* L. and *C. capreolus* L. were around 2.6 and 1.1 per km², respectively (Čermák et al. 2009; Suchomel et al. 2010). Based on the long-term monitoring by a local

hunting community, deer densities were stable over the study period of 2014–2016 (personal communication).

Data collection

Tree seedlings were inventoried yearly in the early autumn over the period of 2014–2016 on 98 circular permanent inventory plots (2 m² corrected for slope) regularly spaced 44.25 m apart. Seedlings on inventory plots were identified to species level and grouped into the following height classes: <0.15, 0.15–0.49 and 0.5–1.3 m (Online Resource 2 Fig. S1–S3, Table S1).

In 2014, we also mapped seedlings < 1 cm DBH on a 110 m × 8 m transect in the north-northeast part of the reserve. These seedlings were identified to species, and their height was measured up to a terminal bud to the nearest 0.5 cm. Deer browsing from the past winter and current growing seasons (i.e. only current-year browsing signs) was recorded for all seedlings on inventory plots and transect if a leader shoot or more than 20% of lateral shoots were browsed.

Analysis of seedling inventory data

The probability of a browsing event (Question 1)

To investigate how the probability of a browsing event was related to forage quantity (seedling density) and quality (species and height class of seedlings), we fitted a generalized linear mixed model with a binomial error distribution and logit link function (Bolker et al. 2009), using the seedling inventory dataset (Table 3, Online Resource 2 Fig. S4, S5). The occurrence of a browsing event (a 0/1 binary response) was related to the fixed effects of conspecific seedling density per height class, height class, year, species, and the interaction of conspecific seedling density and species (Table 3). An inventory plot was used as a random intercept to account for variation in the occurrence of browsing events among inventory plots. The interaction of conspecific seedling density and species was included because we expected interspecific differences in density-dependent browsing (Liang and Seagle 2002; Kim and Underwood 2015). Although we initially considered the interaction of conspecific seedling density and height class, it was excluded in the subsequent analysis as unimportant based on the results of a likelihood ratio test comparing the models with and without this interaction term. Despite being statistically insignificant, inventory year was included in the model as an intrinsic part of the study design.

Seedling density was calculated for each height class and species as the number of seedlings per inventory plot. Conspecific seedling density was standardized prior to analyses by subtracting its mean value and dividing by one standard

Table 1 Overview of research questions and corresponding datasets, analyses, null hypotheses, species included in the analyses, figures and tables

No	Question	Data	Sampling year	Main analyses	Null hypothesis	Species analysed	Figures, tables
(1)	How does the probability of a browsing event vary depending on the species, sizes and densities of seedlings, and are the effects of seedling density species-specific??	Seedling inventory	2014, 2015, 2016	Generalized linear mixed model	Model parameters (fixed effects) are not different from zero	Beech, fir, maple	Figure 1, Table 2, 3
(2)	Do spatial relationships of browsed and unbrowsed seedlings indicate deer foraging preferences for particular species?	Seedling transect	2014	Spatial point pattern analyses	Pair correlation functions	Beech, fir	Figure 2
(3)	Do seedlings become resistant/susceptible to deer browsing depending on the proximity to conspecific and hetero-specific seedlings?	Seedling transect	2014		Mark connection functions	Beech, fir	Figure 3
(4)	Are seedling sizes spatially correlated with unbrowsed and browsed seedlings, indicating deer foraging preferences for certain sizes?	Seedling transect	2014		Mark correlation functions	Beech, fir	Figure 4, 5

deviation. The binary response (the occurrence of a browsing event) was converted from conspecific seedling densities. Specifically, a browsing event occurred only if conspecific seedling density was >0 and at least one seedling of a species and respective height class was browsed (i.e. the conspecific density of browsed seedlings per height class was >0). We further pooled the data from the 0.15–0.49 and 0.5–1.3 m height classes as there were only few seedlings in the latter height class (Online Resource 2 Fig. S3, Table S1). As a result, seedlings in the <0.15 m height class were considered small, while seedlings in the 0.15–1.3 m height class tall. Beech, fir and maple were used for the analysis, and spruce was excluded for a lack of data. The analyses with generalized linear mixed models were carried out in the R statistical software (R Core Team 2020) using the library glmmTMB (Magnusson et al. 2017).

Analysis of seedling transect data

Spatial relationship between browsed and unbrowsed seedlings (Question 2)

Using the seedling transect dataset, we employed spatial point pattern analysis to characterize the spatial relationship between browsed and unbrowsed seedlings of each species, represented by a univariate (single-species) spatial point pattern of browsed and unbrowsed seedlings. The seedling patterns of only beech and fir from the seedling transect dataset were used for spatial point pattern analyses (Table 1). Other species (spruce, maple) with less than 50 seedlings were excluded because such a low number of seedlings (points) precludes meaningful spatial point pattern analyses (Wiegand and Moloney 2014).

To analyse the spatial point pattern of browsed and unbrowsed seedlings, we adopted several variants of univariate and bivariate pair correlation functions. The pair correlation function $g(r)$ can be defined as the probability of observing a pair of points separated by a distance r , divided by the corresponding probability for a Poisson process (Baddeley et al. 2015). As a non-cumulative test statistic, this evaluates only the pairs of points separated by a certain distance r . It is therefore useful for studying the properties of a spatial point pattern over a continuous range of distances (Wiegand and Moloney 2004).

We used multiple summary statistics to provide a more comprehensive understanding of the underlying spatial processes (Wiegand and Moloney 2014). Deer browsing was a qualitative (categorical) mark, representing the binary property of each point (browsed/unbrowsed seedling). In the first step, we examined whether deer browsing was a random process and identified any potential departure from this random process. The random process was represented by the random labelling null model, assuming that there is no

spatial correlation among browsed and unbrowsed seedlings. This is particularly useful if we are not interested in the processes which a priori generated the spatial point pattern of seedlings (e.g. seed dispersal, habitat filtering), but rather in the processes, such as deer browsing, which acted a posteriori over the existing point pattern and ultimately resulted in deer selections of seedlings for browsing (Wiegand and Moloney 2014). We used the following three test statistics in which the subscript b stands for a “browsed” seedling and u for an “unbrowsed” seedling: (1) the univariate $g_{bb}(r)$ and (2) $g_{uu}(r)$ functions (one type of points per function) to detect the clustering/hyperdispersion of browsed and unbrowsed seedlings, respectively, (3) the bivariate $g_{bu}(r)$ function (two types of points per function) to detect the aggregation/segregation of browsed and unbrowsed seedlings (Wiegand and Moloney 2014). The values above/below the simulation envelopes indicate the clustering/hyperdispersion of browsed seedlings (g_{bb}), clustering/hyperdispersion of unbrowsed seedlings (g_{uu}) and aggregation/segregation of browsed and unbrowsed seedlings (g_{bu}). If the values of these functions overlap the simulation envelopes it indicates that respective seedlings are randomly distributed (i.e. density-independent browsing).

We ran 199 Monte Carlo simulations to test whether the test statistics fell outside the stochastic range of the random labelling and independent marking null models, with the fifth lowest and the fifth highest simulations at a given scale representing the 95% simulation envelopes (Wiegand and Moloney 2014). All test statistics were evaluated every ten centimetres up to a distance of 4 m. We selected the 4 m distance as a cut-off (i.e. half of the shortest side of the transect), because the estimation of test statistics could be biased due to edge effects beyond this distance (Wiegand and Moloney 2014).

The seedling marks were randomly shuffled over the univariate pattern of unbrowsed and browsed seedlings while keeping the point locations fixed (Goreaud and Pélissier 2003). As a complementary method, a goodness-of-fit test based on a Cramer–von Mises type statistic (Loosmore and Ford 2006) was also performed for the whole range of studied distance intervals up to 4 m. Spatial point pattern analyses were run in the Programita software (Wiegand and Moloney 2004, 2014).

The spatial effect of seedling neighbours on browsing probability (Question 3)

We examined whether the probability of browsing increased or decreased as a function of distance to conspecific and/or heterospecific neighbours, using the multivariate mark connection function $p_{a,b}(r)$. This is a multivariate function because we studied if an “antecedent” point pattern of seedling neighbours a influenced the univariate point pattern of

browsed b and unbrowsed u seedlings. This type of multivariate spatial point pattern analysis is also referred to as trivariate random labelling as there were three types of points involved (a , b and u), and random labelling was used as a null model (see Online Resource 1 for formulas). To examine different types of density-dependent neighbourhood effects, we used the two variants of the mark connection function $p_{a,b}(r)$ in which the “antecedent” point pattern of seedling neighbours a was separately represented by conspecific ($p_{\text{con},b}$) and heterospecific seedlings ($p_{\text{het},b}$). The values of $p_{\text{con},b}(r)$ and $p_{\text{het},b}(r)$ above/below the simulation envelopes indicate that browsing probability increases/decreases as a function of distance to respective seedling neighbours.

Spatial correlation of seedling sizes (Question 4)

To reveal if deer preferred different seedling sizes of a species, we employed the bivariate mark correlation function for univariate (single-species) point patterns. More specifically, we analysed whether seedling sizes (quantitative mark), m_u for unbrowsed seedlings and m_b for browsed seedlings, were spatially correlated with the spatial point patterns of browsed and unbrowsed seedlings (qualitative mark). For example, this could reveal if deer showed foraging preferences for seedling sizes of a species, i.e. whether the sizes of one type of point (e.g. browsed seedlings) tended to be smaller or taller than expected near another type of point (e.g. unbrowsed seedlings). We estimated the mean value $c_{bu,t}(r)$ of a corresponding test function taken over all pairs i – j of seedlings separated by the distance r , given that the focal point is of type u (unbrowsed) and the second of type b (browsed). This non-normalized mark correlation function $c_{bu,t}(r)$ was then normalized to make the final mark-correlation function $k_t(r)$ independent of the mark values and distribution (Online Resource 1). We used two variants of r -mark correlation functions $k_{mu}(r)$ and $k_{mb}(r)$, which are based on test functions yielding the mean mark of type u (unbrowsed) and b points (browsed), respectively, which are the distance r away from the points of another type (see Online Resource 1 for formulas; Illian et al. 2008). The values of $k_{mu}(r)$ and $k_{mb}(r)$ above/below the simulation envelopes indicate that seedlings were taller/smaller than expected.

Moreover, we examined whether unbrowsed and browsed seedlings (neighbouring points of different types) tended to have similar or dissimilar sizes than the sizes of a pair of seedlings (points) taken at random (Wiegand and Moloney 2014). We explored with this approach if deer selected taller seedlings for browsing while leaving close smaller seedling neighbours unbrowsed. For these analyses, we applied the bivariate Schlather’s mark correlation function and its corresponding test statistic I_{mumb} (see Online Resource 1 for formulas) to describe how the marks m (seedling height) of two seedlings of type u (unbrowsed) and b (browsed) separated

by distance r differed from their conditional means $\mu_u(r)$ and $\mu_b(r)$, respectively (Schlather et al. 2004). In contrast to the r -mark correlation functions using the overall mean mark μ_{ub} , the marks of browsed and unbrowsed seedlings were compared to the distance-dependent mean marks $\mu_u(r)$ and $\mu_b(r)$, calculated only for the pairs of points separated by the distance r (Wiegand and Moloney 2014). This is basically a Moran’s I type summary statistic characterizing the spatial covariance between the sizes of seedling pairs (Shimatani 2002). The values of $I_{\text{mumb}}(r)$ above/below the simulation envelopes indicate that seedling sizes were positively/negatively correlated. Moreover, we used the independent marking null model in these analyses to represent the situation of no spatial structure in the marks (seedling heights). This is technically equivalent to random labelling in our analyses, but was used to randomize quantitative instead of qualitative marks (Wiegand and Moloney 2014).

As a robust and non-spatial (unrelated to distances between seedling pairs) complementary method to mark-correlation functions, we tested for the equality of distributions and means of seedling sizes with bootstrap techniques (see Online Resource 1 for details on the method, Online Resource 2 Figure S6). These tests were constructed in the R statistical software (R Core Team 2020) following the procedure for bootstrap hypothesis testing suggested by Efron and Tibshirani (1993).

Results

Analysis of seedling inventory data

Overview

Beech and fir seedlings < 0.15 m tall were less browsed, with less than 10% of browsed seedlings (Table 2, Online Resource 2 Fig. S1). Maple seedlings were more frequently browsed in the same height class, with 9–27% of browsed seedlings (Table 2, Online Resource 2 Fig. S1). Although seedling densities of fir < 0.15 m were highest in comparison to other species (Table 2, Online Resource 2 Fig. S1), beech massively dominated among seedlings > 0.15 m tall (Table 2, Online Resource 2 Fig. S2, S3). Seedlings taller than 0.5 m were almost exclusively beech except in 2015 (Table 2, Online Resource 2 Fig. S3). Fir and maple seedlings 0.15–0.49 m tall were frequently browsed, amounting to 58–86% of all seedlings (Table 2, Online Resource 2 Fig. S2). On the other hand, less than 40% of beech seedlings 0.15–0.49 m tall were browsed in all respective years (Table 2, Online Resource 2 Fig. S2).

The probability of a browsing event (Question 1)

Based on the seedling inventory data, our results show that the probability of a browsing event was higher in tall seedlings compared to small seedlings (Table 3). The probability of a browsing event varied among tree species, with maple being more susceptible to browsing than beech (Table 3) and fir seedlings (estimate = 2.68, SE = 0.65, $p < 0.001$) at mean conspecific seedling densities. However, the probability of a browsing event did not differ between beech and fir seedlings at mean conspecific seedling densities (Table 3). Moreover, interspecific variation in the probability of a browsing event was related to conspecific seedling densities as the interaction between conspecific seedling density and species was significant (likelihood ratio test, $df = 2$, $X^2 = 14.99$, $p < 0.001$, Table 3). The probability rapidly increased at high seedling densities and this increase was significantly larger in fir and maple seedlings than in beech seedlings (Fig. 1, Table 3), and larger in maple seedlings than in fir seedlings (Fig. 1, estimate = 2.35, SE = 0.88, $p < 0.01$).

Analysis of seedling transect data

Overview

Based on the seedling transect data, the results of bootstrap hypothesis testing showed that the sizes of fir and beech seedlings differed both in distributions and

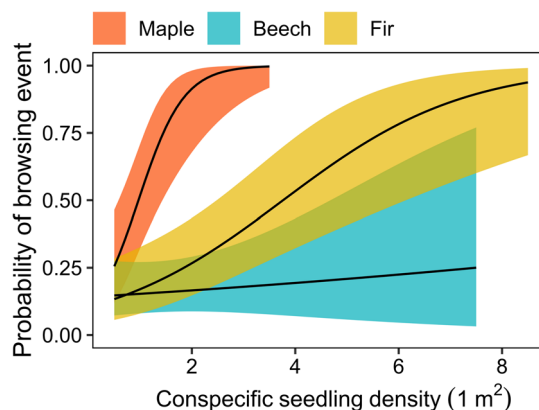


Fig. 1 The effects of conspecific seedling density on the probability of a browsing event in beech, fir and maple seedlings over the period of 2014–2016. Estimated marginal means (predicted probabilities) are related to the interaction between conspecific seedling density and species. The predicted probabilities and 95% confidence intervals are shown only for the observed species-specific ranges of conspecific seedling density. Conspecific seedling density per 1 m² was converted from the original area of 2 m² (area of an inventory plot). Other continuous predictors included in the model (Table 3) were set to their mean value, and factors were set to the average value representing the proportions of each factor's level

means (Online Resource 2 Fig. S6a, d), with fir seedlings (mean = 10.07 cm) being on average smaller than beech seedlings (mean = 25.77 cm). The mean height of browsed beech seedlings was not significantly different from unbrowsed beech seedlings (Fig. 4a, c, Online Resource 2 Fig. S6e), but their heights followed different distributions (Online Resource 2 Fig. S6b). Browsed fir seedlings were on average taller than unbrowsed fir seedlings (Fig. 4b, d, Online Resource 2 Fig. S6f) and their heights also followed different distributions (Online Resource 2 Fig. S6c).

Spatial relationship between browsed and unbrowsed seedlings (Question 2)

We found with the seedling transect data several departures from the random labelling null model in both beech and fir seedlings. Browsed beech seedlings were clustered up to a distance of 2 m (Fig. 2a), whereas browsed fir seedlings were extensively clustered along the whole distance interval up to 4 m (Fig. 2d). We also found that browsed and unbrowsed seedlings were only slightly segregated up to a distance of 0.5 m in fir (Fig. 2e) and slightly aggregated at a distance of 1.5 m in beech (Fig. 2b). While unbrowsed beech seedlings were randomly distributed (Fig. 2c), unbrowsed fir seedlings were hyperdispersed at distances of 0.3–4 m (Fig. 2f).

The spatial effect of seedling neighbours on browsing (Question 3)

Our results of the seedling transect data showed that the probability of browsing increased depending on the distance to conspecific seedlings in both beech and fir seedlings. However, the signs of this density-dependent browsing were relatively weak in beech seedlings and were restricted to the distances of 0.8–1.5 m from conspecific seedlings (Fig. 3a), while they were strong and operated along the whole distance interval up to 4 m in fir seedlings (Fig. 3b).

The probability of browsing also increased with the distance to heterospecific seedlings. However, beech seedlings experienced stronger density-dependent browsing at distances up to 2.2 m from fir seedlings (Fig. 3c). Fir seedlings were, on the other hand, exposed to density-dependent browsing at all distances from beech seedlings (Fig. 3d).

Spatial correlation of seedling sizes (Question 4)

We found with the seedling transect data that unbrowsed beech seedlings were taller than expected given the overall mean height of beech seedlings at distances of 2–4 m from browsed seedlings (Fig. 5a). Conversely, the size of browsed beech seedlings was not related to the proximity to unbrowsed seedlings (Fig. 5b). Unbrowsed fir seedlings were 1.15 times taller at most distances up to 4 m

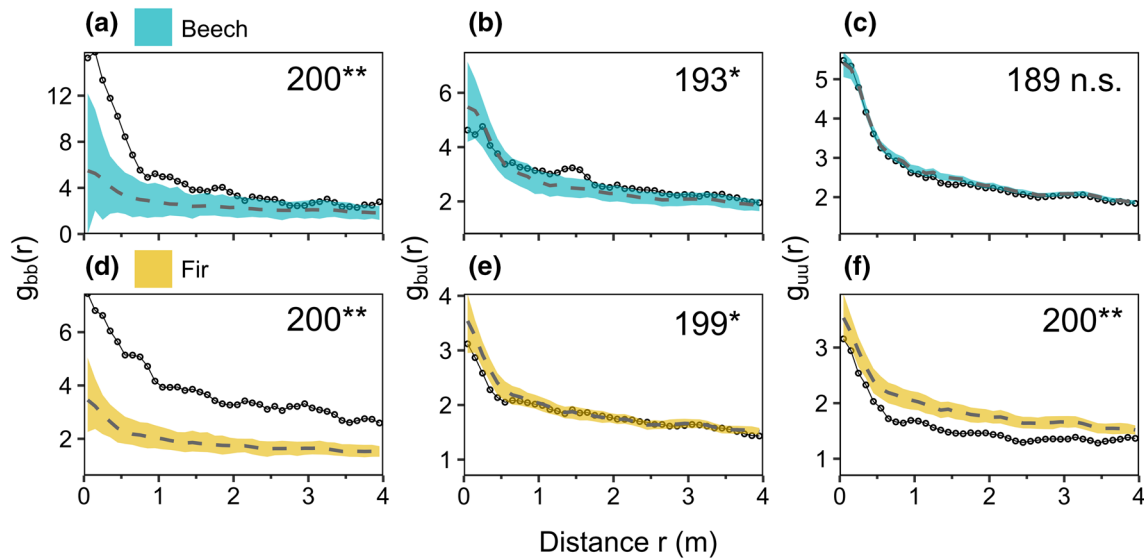


Fig. 2 The results of pair correlation functions to detect potential departures from the random labelling null model in beech (a–c) and fir seedlings (d–f). Summary statistics examine the spatial relationships of browsed seedlings (a, d), browsed and unbrowsed seedlings (b, e) and unbrowsed seedlings (c, f). The values above/below the simulation envelopes indicate the clustering/hyperdispersion of browsed seedlings (g_{bb}), clustering/hyperdispersion of unbrowsed seedlings (g_{uu}) and aggregation/segregation of browsed

and unbrowsed seedlings (g_{bu}). The random labelling null here represents an assumption that deer browsing is a spatially random process unrelated to the distance to seedling neighbours. The 95% simulation envelopes were constructed at a given scale as the fifth largest and fifth smallest value of 199 Monte Carlo simulations. The numbers in each subplot denote the rank of a goodness-of-fit test. Significant departures are indicated by ** and * for p values < 0.01 and < 0.05, respectively

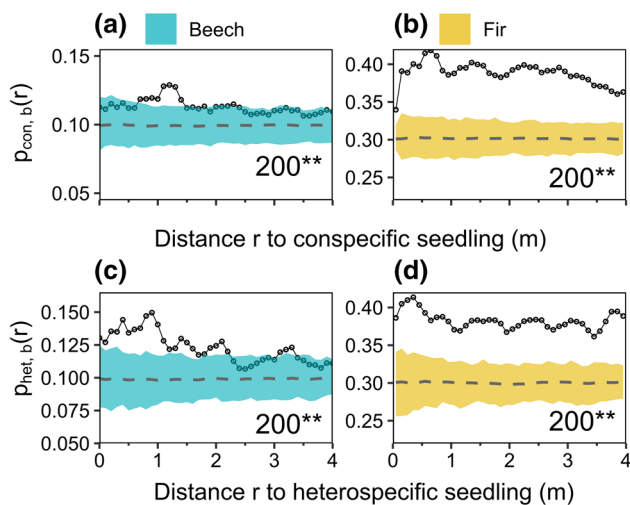


Fig. 3 The results of mark connection functions to examine the browsing probability of beech (a, c) and fir seedlings (b, d) as a function of distance to conspecific ($p_{con, b}$) and heterospecific neighbours ($p_{net, b}$). The values above/below the envelopes indicate that the probability of browsing increases/decreases as a function of distance to seedling neighbours. Other conventions are the same as in Fig. 2

from browsed seedlings (Fig. 5d). However, browsed fir seedlings were ca 1.4 times taller than expected at all distances from unbrowsed seedlings (Fig. 5e). In addition, the sizes of unbrowsed and browsed beech seedlings were

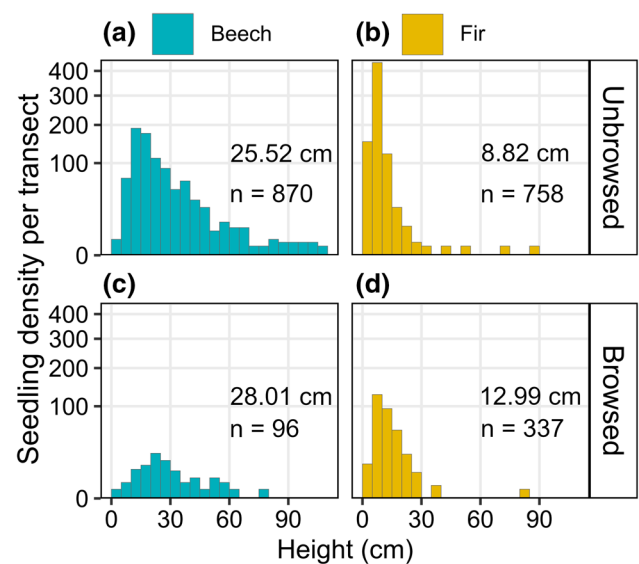


Fig. 4 Histogram of the heights of browsed and unbrowsed seedlings on the seedling transect. Beech (a, c) and fir seedlings (b, d) are displayed. The bin width was set to 5 cm. The two numbers in each subplot denote the mean seedling height and total number of seedlings n

only slightly correlated (Fig. 5c), whereas the sizes of unbrowsed and browsed fir seedlings were positively correlated almost along the whole distance interval (Fig. 5f).

Table 2 The average density of all (All) and browsed seedlings (Browsed) per hectare by species, inventory year and height class

Year	Species	Height class								
		<0.15 m			0.15–0.49 m			0.5–1.3 m		
		All	Browsed	%	All	Browsed	%	All	Browsed	%
2014	Beech	11,954	104	0.9	2610	835	32.0	574	574	100
	Fir	20,462	1148	5.6	574	470	81.9	–	–	–
	Maple	2349	209	8.9	626	418	66.8	–	–	–
2015	Beech	4594	104	2.3	3132	1148	36.7	418	418	100
	Fir	9187	470	5.1	209	157	75.1	104	104	100
	Maple	1514	261	17.2	731	626	85.6	–	–	–
2016	Beech	3028	157	5.2	3758	1409	37.5	418	157	37.6
	Fir	16,129	1148	7.1	574	418	72.8	52	52	100
	Maple	2140	574	26.8	626	365	58.3	–	–	–

The percentage of browsed seedlings (%) is shown in bold. Seedling density per hectare was calculated over all 98 inventory plots (i.e. inventory plots where conspecific seedling densities equalled zero were included) and converted from the original 2-m² area of an inventory plot to represent overall site summaries

Table 3 A generalized linear mixed model relating conspecific seedling density, species and height class of seedlings, inventory year and the interaction (asterisk) of conspecific seedling density and species to the occurrence of a browsing event

Model parameter (fixed effects)	Estimate	SE	2.5% CI	97.5% CI	<i>p</i> value
Intercept	–3.509	0.465	–4.419	–2.56	<0.001
Conspecific seedling density	0.129	0.254	–0.369	0.627	0.612
Species (fir)	0.410	0.428	–0.429	1.25	0.566
Species (maple)	3.088	0.666	1.782	4.394	<0.001
Height class (tall)	3.330	0.408	2.530	4.13	<0.001
Year (2015)	0.199	0.376	–0.538	0.936	0.596
Year (2016)	0.371	0.360	–0.334	1.076	0.303
Conspecific seedling density * species (fir)	0.654	0.326	0.015	1.293	0.045
Conspecific seedling density * species (maple)	3.003	0.911	1.217	4.79	<0.001

P-values in bold indicate significant effects (<0.05). Beech, the height class of small seedlings (<0.15 m) and 2014 inventory year were set as reference levels. Inventory plot was used as a random intercept. The model summary includes parameter estimates (Estimate), standard errors (SE), lower and upper bounds of 95% confidence intervals (CI), and *p*-values. As three factors (Height class, Species and Year) were included in the model, the intercept is the mean estimate of the group that represents the reference level for all factors (small beech seedlings in 2014 in this case). Individual species estimates are interpretable only for the mean conspecific seedling density because of the interaction in the model

Discussion

Our findings illustrate that deer foraging decisions acting at fine spatial scales are substantially influenced by different types of neighbourhood effects, i.e. by the effects of conspecific and heterospecific seedling neighbours on the susceptibility of a focal seedling to deer herbivory. Building on the premise that neighbourhood effects are related to the distance to and density of seedling neighbours, we show they may indicate the strength and spatial extent of deer foraging selectivity for a particular tree species.

Neighbourhood effects on deer browsing—the evidence from a seedling inventory

Based on the results of a seedling inventory, the strongest density-dependent browsing was targeted to maple seedlings, indicating that this species was frequently utilized by deer even at relatively low conspecific densities. While deer were also highly responsive to the availability of fir seedlings, beech experienced relatively weak density-dependent browsing compared to maple and fir seedlings. Even though this generally corresponds to deer preferences that have already frequently been described (Ammer 1996; Klopčič et al.

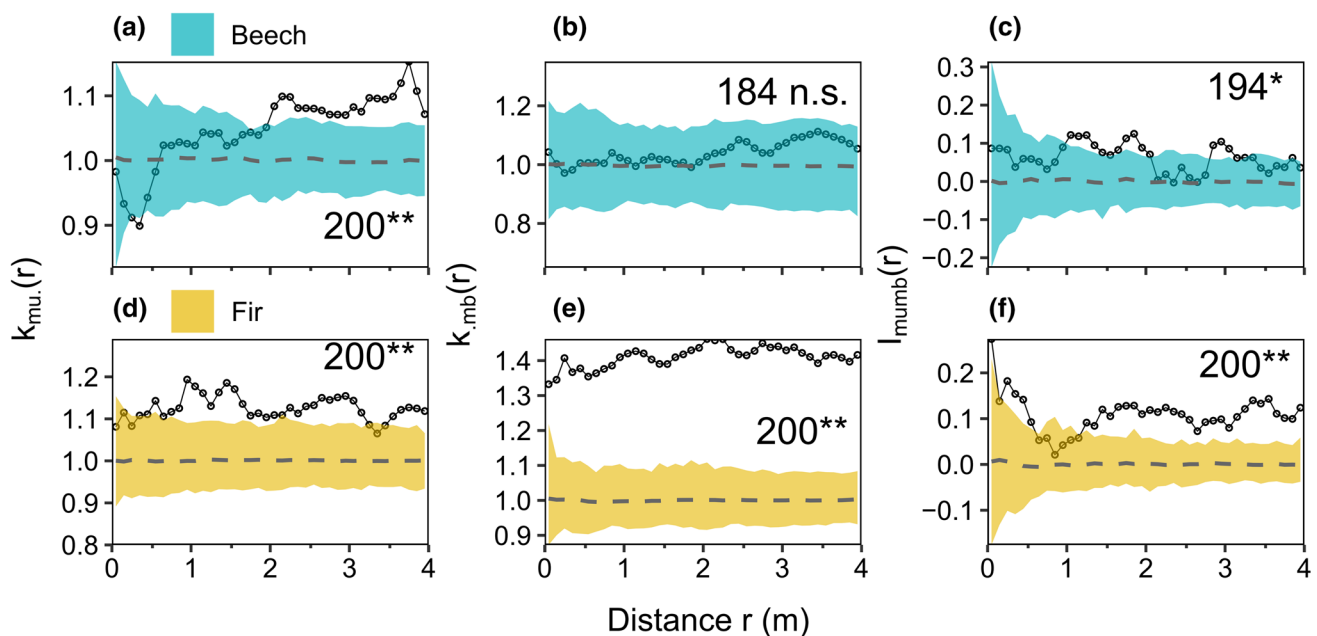


Fig. 5 The results of several bivariate r -mark correlation functions ($k_{\text{mu.}}$, k_{mb}) and Schlather's test functions (I_{mumb}) to examine the spatial correlation of seedling height with the point patterns of browsed and unbrowsed beech (a–c) and fir (d–f) seedlings. The functions $k_{\text{mu.}}$ and k_{mb} yield the normalized mean mark of unbrowsed and browsed seedlings, respectively, which are distance r away from the seedlings of another type. The independent marking null model here represents

the assumption of no spatial correlation in seedling heights, i.e. deer selection of seedling heights was a spatially random process unrelated to the distance to seedling neighbours. The values above/below the envelopes indicate that seedlings were taller/smaller than expected (r -mark correlation functions) and seedling sizes were positively/negatively correlated (Schlather's test functions). Other conventions are the same as in Fig. 2

2010; Simončič et al. 2019), we show that seedling density of species may differentially shape deer foraging decisions when feeding within patches of tree seedlings. For example, there could be only one maple seedling per 1 m^2 for a browsing probability of less than 50%, while three fir and even five beech seedlings could occur per 1 m^2 to remain below the same probability threshold. It thus seems that deer were very sensitive to the density of the highest quality food (maple), while other, relatively less preferred species (fir and beech), were exploited once they became more abundant in a patch. In a study in a riparian forest, such interspecific differences in density-dependent browsing were also observed for the seedlings of woody species, although the relationship between browsing intensity and relative species density was used as a measure for the level of browsing impact on seedling populations (Liang and Seagle 2002).

Scaling neighbourhood effects—the evidence from a seedling transect

We show that multiple neighbourhood effects of different strength and spatial extent shaped deer foraging behaviour at the spatial scales of seedling neighbourhoods, which, in turn, determined how deer browsing was spatially distributed among beech and fir seedlings. When neighbours were

conspecific, fir seedlings experienced spatially extensive and strong density-dependent browsing, indicated by extensive clustering of browsed fir seedlings and a higher browsing probability at all distances from conspecific seedlings. In contrast, browsed beech seedlings exhibited much less spatially extensive clustering, and the browsing probability was only slightly associated with the distance to conspecific seedlings, indicating weak density-dependent browsing. This is consistent with the findings from the seedling inventory because the tree species, here beech and fir, were exposed to different strengths of density-dependent deer foraging selectivity. However, not only the strength but also the spatial extent of this density-dependent browsing differed between beech and fir seedlings.

To interpret this in more detail, if fir seedlings occurred at different distances from each other, they tended to be selected by deer and formed aggregations more frequently than would be expected if deer browsed seedlings randomly. On the other hand, if beech seedlings occurred at different distances from each other, browsed beech seedlings were clustered at only short distances and were selected mostly irrespective of other conspecific seedlings, indicating that browsing of beech seedlings was non-random (selective) within short distances, but became random (opportunistic) as the effect of conspecific beech neighbours did not modify

deer foraging decisions beyond these short distances. It thus seems that deer showed relatively low interest in a spatially extensive selection of beech seedlings, while the opposite was true for fir seedlings. In the light of foraging theory, these findings suggest that a resource concentration effect was an important component of deer foraging behaviour at the spatial scales of seedling neighbourhoods (Root 1973; Hämbäck et al. 2014), especially in terms of the browsing of fir seedlings. In contrast to our findings, a study from the Alps showed that fir seedlings were browsed opportunistically as the consumption of fir seedlings was unrelated to their availability and increased only near palatable herbaceous vegetation (Häsler and Senn 2012). We think that this difference may be attributed to the low abundance of other palatable vegetation at our site (although not explicitly addressed in our study), which possibly made deer exploit more common tree seedlings, as well as to the use of a different metric for gauging the availability of fir seedlings (Häsler and Senn 2012). Moreover, the dissimilar spatial scales at which the relationship between herbivory and food resource availability was quantified could play a role, because this relationship may be unimportant or difficult to detect at some spatial scales (Champagne et al. 2016). Although deer randomly selected beech seedlings at most distances, the resource dilution effect, suggesting a density-dependent deer foraging avoidance of seedlings, was not observed in our study (Otway et al. 2005). This neighbourhood effect probably becomes more important once a plant species is particularly unpalatable or defended (Baraza et al. 2006).

Moreover, the fact that beech seedlings were browsed mostly irrespective of the distance to and density of conspecific neighbours suggests that the selection of beech seedlings to be browsed by deer may result from the fact that deer usually do not only consume food of higher quality, such as maple or fir in our study, especially when the diet is mixed (Alm et al. 2002). The reason why one tree species is consumed opportunistically while another is selectively preferred is usually explained by the benefits of diet mixing, because nutrient requirements are more likely fulfilled when consuming multiple plant types (Wiggins et al. 2006; Ohse et al. 2017b), or by seasonal variation in food abundance and quality, making deer consume even lower quality food resources (Moser et al. 2006; Storms et al. 2008).

Another reason why a species is or is not browsed may depend on the characteristics of heterospecific neighbours, because heterospecific species are expected to have more contrasting traits compared to intraspecific variation in traits of a focal species (Bergvall et al. 2006; Underwood et al. 2014). Our findings suggest that neighbourhood effects of heterospecific seedlings (i.e. associational effects; Barbosa et al. 2009; Hämbäck et al. 2014; Underwood et al. 2014) influenced the strength and spatial extent of deer foraging selectivity for beech and fir seedlings. We found that beech

seedlings tended to be more likely browsed near fir neighbours than would be expected for random deer foraging decision, suggesting that associational susceptibility could elevate the foraging selectivity for beech seedlings at these fine neighbourhood scales. Moreover, beech seedlings were more likely browsed at short distances from fir neighbours, as opposed to beech neighbours that induced almost no change in the browsing probability of focal beech seedlings. Beech seedlings similarly experienced associational susceptibility with the increasing density of more palatable *Betula* in lowland temperate forests (Bobrowski et al. 2015). In another study, *Betula* individuals were browsed by deer only when they were near more palatable *Salix* individuals, while patches comprised only of *Betula* were not foraged (Bergman et al. 2005). In general, plants in a patch of high forage quality may experience this type of negative neighbourhood effect (Pietrzykowski et al. 2003; Bergvall et al. 2006; Bee et al. 2009). Moreover, patches with a high abundance of beech seedlings were less preferred by deer at larger spatial scales in a mixed temperate forest, suggesting that beech seedlings may give rise to associational resistance influencing deer foraging decisions between patches (Ohse et al. 2017b). This is interesting because beech seedlings were the least preferred tree species at our site, and thus we might expect that beech neighbours would give rise to associational resistance when the focal species is more attractive to deer (Bee et al. 2009). However, associational effects are scale-dependent and thus could operate at different scales than in our study (Barbosa et al. 2009; Champagne et al. 2016). Associational resistance is usually expected to arise at larger spatial scales corresponding to foraging decisions made on the level of patches or herbivore home ranges (Bergvall et al. 2006; Champagne et al. 2016). At the fine spatial scale of seedling neighbourhoods, we found that fir seedlings experienced browsing more frequently in the proximity of beech neighbours, indicating that beech seedlings could attract deer and increase the browsing probability of fir seedlings similarly as conspecific neighbours. Thus, our findings are more consistent with a situation when attractive seedlings (fir) become more frequently browsed near less preferred neighbours (beech), which has previously been termed as the neighbour contrast susceptibility (Bergvall et al. 2006). This is technically also associational susceptibility, but the role of attractive and less preferred species is now reversed, with the attractive and not the less preferred species receiving the negative outcomes of this neighbourhood effect. However, it is questionable whether beech neighbours truly influenced the browsing of fir seedlings via neighbour contrast susceptibility, or if this was falsely detected owing to high local seedling densities and spatial aggregation with other species (especially fir), which in fact attracted deer and consequently influenced the browsing of fir seedlings. This highlights the challenges for future research, as experimental testing is

needed to control for the effects of focal species density, neighbour density/frequency and total density in order to correctly characterize associational effects in plant–herbivore interactions (Underwood et al. 2014).

Moreover, it is surprising that associational susceptibility increased deer browsing of beech seedlings near fir seedling neighbours at fine spatial scales, as this is generally more likely to be expected at larger spatial scales when foraging decisions are made between patches (Bergvall et al. 2006). It may be that differences in the scale dependence of individual associational effects are in fact minor (Champagne et al. 2016), or perhaps some other factors may be necessary for different associational effects to arise. Although this could not be examined in our study with a single site, how herbivore densities are limited by spatial variation in food availability within their effective foraging capacities (e.g. home ranges) may be an important factor for herbivores when deciding at which spatial scale it is optimal to make foraging decisions (Hjältén et al. 1993; Bee et al. 2009). This, in turn, may determine the strength and type of neighbourhood effects (Baraza et al. 2006). Nevertheless, other studies have demonstrated that associational susceptibility can operate at relatively fine spatial scales, for instance that deer exploited less preferred *Calluna vulgaris* more up to several meters from grass-patch edges (Hester and Baillie 1998; Palmer et al. 2003), as well as at larger spatial scales (Milligan and Koricheva 2013).

Spatial distributions of unbrowsed seedlings and seedling sizes

Our findings show that the odds that deer would avoid fir seedlings were quite low at the scales of seedling neighbourhoods, with random or almost no spatial separation between browsed and unbrowsed seedlings, i.e. between the deer foraging decisions leading to seedlings becoming browsed and being avoided or unnoticed by deer. The potential avoidance of browsing seems, if at all, to occur at different and probably larger spatial scales, e.g. at scales of whole forest types (Kupferschmid 2018).

It remains to be answered what mechanism could lead to the spatial regularity of unbrowsed fir seedlings. We think that either deer passed by these seedlings unnoticed or they were generally less attractive to deer for some reason, with the latter scenario being more likely because deer are usually very selective in their foraging behaviour (Storms et al. 2008; Abbas et al. 2011). Some proportion of seedlings could also be avoided, as it is not common for herbivores to deplete all the available resources due to spatial and seasonal variation in the quality of browsed plants (Häsler et al. 2008; Storms et al. 2008). However, these avoided unbrowsed fir seedlings were found to be smaller on average than browsed ones, confirming that deer usually prefer vigorously growing

and tall seedlings, and small and suppressed ones are mostly avoided (Häsler and Senn 2012; Kupferschmid et al. 2013). This was true especially for fir seedlings but less for beech seedlings, because browsed fir seedlings were mostly taller near unbrowsed seedlings, indicating that taller seedlings were largely preferred by deer and nearby smaller seedlings avoided or unnoticed. We thus show that the selection of tall fir seedlings for browsing may occur at the scales of seedling neighbourhoods, although vegetation size is likely an important criterion even for between-patch deer foraging decisions at larger spatial scales (Pietrzykowski et al. 2003; Miller et al. 2006). However, as browsing of fir seedlings may be highest in winter (Häsler and Senn 2012), selecting small seedlings may not even be an option if they are covered by snow (Visscher et al. 2006). Similarly, tall neighbouring vegetation could also impede the search and selection for smaller seedlings due to lower seedling apparency (Pietrzykowski et al. 2003; Miller et al. 2006). While snow cover could be an important factor influencing what size of seedlings deer selected at our site, we think that vegetation other than tree seedlings did not play much of a role in deer foraging decisions as they were generally scarce and short on the seedling transect.

In contrast to fir seedlings, browsing selectivity was usually not related to the height of beech seedlings, pointing to the fact that the size of beech seedlings itself was not likely an important criterion for deer in deciding which beech seedling to browse. This again demonstrates opportunistic deer foraging selectivity for beech seedlings, while fir seedlings were subject to highly selective foraging both in terms of seedling sizes and densities. However, factors other than browsing likely played a role in shaping the height structure of fir seedlings. For instance, seedling sizes may correspond to variation in environmental conditions represented, e.g. by the gradient of light availability, and could thus explain positive correlations between the sizes of seedlings (Rozenbergar et al. 2007). Whatever the reason, browsed and unbrowsed fir seedling pairs were still more similar than expected at most distances in our study.

Conclusions

Our findings illustrate that the neighbourhood effects of seedlings modified deer foraging behaviour depending on the proximity, density and species identity of seedling neighbours, which, in turn, determined the strength and spatial extent of browsing impacts on beech and fir seedlings. We therefore suggest that when the spatial scale is not explicitly considered in studies of neighbourhood effects on plant–herbivore interactions, herbivore foraging decisions underlying neighbourhood effects and consequent herbivory impacts on plant populations may be

difficult to predict and can hardly be compared to other foraging environments or the foraging behaviour of different herbivores. In addition, by ignoring the spatial extent of neighbourhood effects, inferences about the role of different plant neighbours in shaping herbivore foraging decisions may be incomplete and potentially biased, similar to what has been shown in studies of neighbourhood effects on plant survival and growth (Zambrano et al. 2019; Furniss et al. 2020).

We conclude that using the neighbourhood effects of beech seedlings to prevent fir seedlings from deer browsing may not meet with success at the spatial scales of seedling neighbourhoods owing to strong deer foraging selectivity for fir seedlings both near conspecific and beech neighbours. However, this needs further investigation in terms of browsing intensity, as less-preferred plant neighbours may not prevent deer from browsing fir seedlings, but could potentially reduce browsing damage (Milligan and Koricheva 2013). Therefore, studying how the spatial distribution of herbivore damage is influenced by different types of neighbourhood effects should be the next step towards better understanding how and at which spatial scales they could be applied to prevent excessive deer herbivory, e.g. in commercial forestry or conservation management (Palmer et al. 2003; Underwood et al. 2014; Ohse et al. 2017b). Finally, vegetation other than tree seedlings must be considered at sites where, e.g. shrubs or herbaceous plants may influence herbivory on the focal plant species (Pietrzykowski et al. 2003; Baraza et al. 2006).

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Compliance with ethical standards

Conflict of interest The authors declare no conflicts of interest.

Consent to participate All authors agreed to participate in the work presented in this manuscript.

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Availability of data Data are available from the corresponding author on request.

References

- Abbas F, Morellet N, Hewison AJM, Merlet J, Cargnelutti B, Lourtet B, Angibault JM, Daufresne T, Aulagnier S, Verheyden H (2011) Landscape fragmentation generates spatial variation of diet composition and quality in a generalist herbivore. *Oecologia* 167:401–411. <https://doi.org/10.1007/s00442-011-1994-0>
- Alm U, Birgersson B, Leimar O (2002) The effect of food quality and relative abundance on food choice in fallow deer. *Anim Behav* 64:439–445. <https://doi.org/10.1006/anbe.2002.3057>
- Ammer C (1996) Impact of ungulates on structure and dynamics of natural regeneration of mixed mountain forests in the Bavarian Alps. *For Ecol Manage* 88:43–53. [https://doi.org/10.1016/s0378-1127\(96\)03808-x](https://doi.org/10.1016/s0378-1127(96)03808-x)
- Arditi R, Dacorogna B (1988) Optimal foraging on arbitrary food distributions and the definition of habitat patches. *Am Nat* 131:837–846. <https://doi.org/10.1086/284825>
- Atsatt PR, O'Dowd DJ (1976) Plant defense guilds. *Science* 193:24–29. <https://doi.org/10.1126/science.193.4247.24>
- Baddeley A, Rubak E, Turner R (2015) Spatial point patterns: methodology and applications with R. Chapman and Hall/CRC, London
- Bailey DW, Gross JE, Laca EA, Rittenhouse LR, Coughenour MB, Swift DM, Sims PL (1996) Mechanisms that result in large herbivore grazing distribution patterns. *J Range Manag* 49:386–400. <https://doi.org/10.2307/4002919>
- Baraza E, Zamora R, Hodar JA (2006) Conditional outcomes in plant–herbivore interactions: neighbours matter. *Oikos* 113:148–156. <https://doi.org/10.1111/j.0030-1299.2006.14265.x>
- Barbosa P, Hines J, Kaplan I, Martinson H, Szczepaniec A, Szendrei Z (2009) Associational resistance and associational susceptibility: having right or wrong neighbors. *Annu Rev Ecol Evol Syst* 40:1–20. <https://doi.org/10.1146/annurev.ecolsys.110308.120242>
- Beckerman AP, Oksanen L (2005) The shape of things eaten: the functional response of herbivores foraging adaptively. *Oikos* 110:591–601. <https://doi.org/10.1111/j.0030-1299.2005.13546.x>
- Bee JN, Tanentzap AJ, Lee WG, Lavers RB, Mark AF, Mills JA, Coomes DA (2009) The benefits of being in a bad neighbourhood: plant community composition influences red deer foraging decisions. *Oikos* 118:18–24. <https://doi.org/10.1111/j.1600-0706.2008.16756.x>
- Bergman M, Iason GR, Hester AJ (2005) Feeding patterns by roe deer and rabbits on pine, willow and birch in relation to spatial arrangement. *Oikos* 109:513–520. <https://doi.org/10.1111/j.0030-1299.2005.13794.x>
- Bergvall UA, Rautio P, Kesti K, Tuomi J, Leimar O (2006) Associational effects of plant defences in relation to within- and between-patch food choice by a mammalian herbivore: neighbour contrast susceptibility and defence. *Oecologia* 147:253–260. <https://doi.org/10.1007/s00442-005-0260-8>
- Bobrowski M, Gillich B, Stolter C (2015) Modelling browsing of deer on beech and birch in northern Germany. *For Ecol Manage* 358:212–221. <https://doi.org/10.1016/j.foreco.2015.08.031>
- Bolker BM, Brooks ME, Clark CJ, Geange SW, Poulsen JR, Stevens MHH, White JSS (2009) Generalized linear mixed models: a practical guide for ecology and evolution. *Trends Ecol Evol* 24:127–135. <https://doi.org/10.1016/j.tree.2008.10.008>

- Čermák P, Horsák P, Špiřík M, Mrkva R (2009) Relationships between browsing damage and woody species dominance. *J For Sci* 55:23–31. <https://doi.org/10.17221/73/2008-JFS>
- Champagne E, Tremblay JP, Côté SD (2016) Spatial extent of neighboring plants influences the strength of associational effects on mammal herbivory. *Ecosphere* 7:13. <https://doi.org/10.1002/ecs2.1371>
- Connell JH (1971) On the role of natural enemies in preventing competitive exclusion in some marine animals and in rain forest trees. In: Den Boer PJ, Gradwell GR (eds) *Dynamics of populations*. Centre for Agricultural Publishing and Documentation, Wageningen, pp 298–312
- Danell K, Edenius L, Lundberg P (1991) Herbivory and tree stand composition—moose patch use in winter. *Ecology* 72:1350–1357. <https://doi.org/10.2307/1941107>
- Efron B, Tibshirani R (1993) *An introduction to the bootstrap*. Chapman and Hall, New York
- Forrister DL, Endara MJ, Younkun GC, Coley PD, Kursar TA (2019) Herbivores as drivers of negative density dependence in tropical forest saplings. *Science* 363:1213. <https://doi.org/10.1126/science.aau9460>
- Fryxell JM, Hazell M, Borger L, Dalziel BD, Haydon DT, Morales JM, McIntosh T, Rosatte RC (2008) Multiple movement modes by large herbivores at multiple spatiotemporal scales. *Proc Natl Acad Sci USA* 105:19114–19119. <https://doi.org/10.1073/pnas.0801737105>
- Furniss TJ, Larson AJ, Kane VR, Lutz JA (2020) Wildfire and drought moderate the spatial elements of tree mortality. *Ecosphere* 11:e03214. <https://doi.org/10.1002/ecs2.3214>
- Gaustad AO, Loe LE, Myserud A (2013) Inferring spatial memory and spatiotemporal scaling from GPS data: comparing red deer *Cervus elaphus* movements with simulation models. *J Anim Ecol* 82:572–586. <https://doi.org/10.1111/1365-2656.12027>
- Goreaud F, Pélissier R (2003) Avoiding misinterpretation of biotic interactions with the intertype K_{12} -function: population independence vs. random labelling hypotheses. *J Veg Sci* 14:681–692. <https://doi.org/10.1111/j.1654-1103.2003.tb02200.x>
- Hämbäck PA, Björkman M, Rämert B, Hopkins RJ (2009) Scale-dependent responses in cabbage herbivores affect attack rates in spatially heterogeneous systems. *Basic Appl Ecol* 10:228–236. <https://doi.org/10.1016/j.baec.2008.06.004>
- Hämbäck PA, Inouye BD, Andersson P, Underwood N (2014) Effects of plant neighborhoods on plant–herbivore interactions: resource dilution and associational effects. *Ecology* 95:1370–1383. <https://doi.org/10.1890/13-0793.1>
- Häsler H, Senn J (2012) Ungulate browsing on European silver fir *Abies alba*: the role of occasions, food shortage and diet preferences. *Wildl Biol* 18:67–74. <https://doi.org/10.2981/09-013>
- Häsler H, Senn J, Edwards PJ (2008) Light-dependent growth responses of young *Abies alba* to simulated ungulate browsing. *Funct Ecol* 22:48–57. <https://doi.org/10.1111/j.1365-2435.2007.01346.x>
- Hester AJ, Baillie GJ (1998) Spatial and temporal patterns of heather use by sheep and red deer within natural heather/grass mosaics. *J Appl Ecol* 35:772–784. <https://doi.org/10.1046/j.1365-2664.1998.355348.x>
- Hjältén J, Danell K, Lundberg P (1993) Herbivore avoidance by association—vole and hare utilization of woody plants. *Oikos* 68:125–131. <https://doi.org/10.2307/3545317>
- Illian J, Penttinen A, Stoyan H, Stoyan D (2008) *Statistical analysis and modelling of spatial point patterns*, 1st edn. Wiley, Chichester
- Illius AW, Duncan P, Richard C, Mesochina P (2002) Mechanisms of functional response and resource exploitation in browsing roe deer. *J Anim Ecol* 71:723–734. <https://doi.org/10.1046/j.1365-2656.2002.00643.x>
- Janzen DH (1970) Herbivores and the number of tree species in tropical forests. *Am Nat* 104:501–528. <https://doi.org/10.1086/282687>
- Jarnemo A, Minderman J, Bunnefeld N, Zidar J, Månsson J (2014) Managing landscapes for multiple objectives: alternative forage can reduce the conflict between deer and forestry. *Ecosphere* 5:1–14. <https://doi.org/10.1890/ES14-00106.1>
- Kim TN, Underwood N (2015) Plant neighborhood effects on herbivory: damage is both density and frequency dependent. *Ecology* 96:1431–1437. <https://doi.org/10.1890/14-1097.1>
- Klopčič M, Jerina K, Bončina A (2010) Long-term changes of structure and tree species composition in Dinaric uneven-aged forests: are red deer an important factor? *Eur J For Res* 129:277–288. <https://doi.org/10.1007/s10342-009-0325-z>
- Kupferschmid AD (2018) Selective browsing behaviour of ungulates influences the growth of *Abies alba* differently depending on forest type. *For Ecol Manag* 429:317–326. <https://doi.org/10.1016/j.foreco.2018.06.046>
- Kupferschmid AD, Zimmermann S, Bugmann H (2013) Browsing regime and growth response of naturally regenerated *Abies alba* saplings along light gradients. *For Ecol Manag* 310:393–404. <https://doi.org/10.1016/j.foreco.2013.08.048>
- Kupferschmid AD, Butikofer L, Hothorn T, Schwyzer A, Brang P (2020) Ungulate species and abundance as well as environmental factors determine the probability of terminal shoot browsing on temperate forest trees. *Forests* 11:22. <https://doi.org/10.3390/f11070764>
- Law R, Illian J, Burslem D, Gratzler G, Gunatilleke CVS, Gunatilleke I (2009) Ecological information from spatial patterns of plants: insights from point process theory. *J Ecol* 97:616–628. <https://doi.org/10.1111/j.1365-2745.2009.01510.x>
- Liang SY, Seagle SW (2002) Browsing and microhabitat effects on riparian forest woody seedling demography. *Ecology* 83:212–227. <https://doi.org/10.2307/2680133>
- Loosmore NB, Ford ED (2006) Statistical inference using the G or K point pattern spatial statistics. *Ecology* 87:1925–1931. [https://doi.org/10.1890/0012-9658\(2006\)87\[1925:SIUTGO\]2.0.CO;2](https://doi.org/10.1890/0012-9658(2006)87[1925:SIUTGO]2.0.CO;2)
- Magnusson A, Skaug H, Nielsen A, Berg C, Kristensen K, Maechler M, van Benthem K, Bolker B, Brooks M, Brooks MM (2017) Package ‘glmmTMB’. R Package Version 02 0
- Maltoni A, Mariotti B, Tani A, Martini S, Jacobs DF, Tognetti R (2019) Natural regeneration of *Pinus pinaster* facilitates *Quercus ilex* survival and growth under severe deer browsing pressure. *For Ecol Manag* 432:356–364. <https://doi.org/10.1016/j.foreco.2018.09.045>
- Massé A, Côté SD (2012) Linking habitat heterogeneity to space use by large herbivores at multiple scales: from habitat mosaics to forest canopy openings. *For Ecol Manag* 285:67–76. <https://doi.org/10.1016/j.foreco.2012.07.039>
- Michéli E, Schad P, Spaargaren O, Dent D, Nachtergale F (2006) World reference base for soil resources 2006. *World Soil Resour Rep* 103:1–128
- Milchunas DG, Noy-Meir I (2002) Grazing refuges, external avoidance of herbivory and plant diversity. *Oikos* 99:113–130. <https://doi.org/10.1034/j.1600-0706.2002.990112.x>
- Miller AM, McArthur C, Smethurst PJ (2006) Characteristics of tree seedlings and neighbouring vegetation have an additive influence on browsing by generalist herbivores. *For Ecol Manag* 228:197–205. <https://doi.org/10.1016/j.foreco.2006.03.003>
- Miller AM, McArthur C, Smethurst PJ (2007) Effects of within-patch characteristics on the vulnerability of a plant to herbivory. *Oikos* 116:41–52. <https://doi.org/10.1111/j.2006.0030-1299.15331.x>
- Milligan HT, Koricheva J (2013) Effects of tree species richness and composition on moose winter browsing damage and foraging selectivity: an experimental study. *J Anim Ecol* 82:739–748. <https://doi.org/10.1111/1365-2656.12049>
- Morellet N, Van Moorter B, Cargnelutti B, Angibault JM, Lourtet B, Merlet J, Ladet S, Hewison AJM (2011) Landscape composition influences roe deer habitat selection at both home range

- and landscape scales. *Landsc Ecol* 26:999–1010. <https://doi.org/10.1007/s10980-011-9624-0>
- Moser B, Schütz M, Hindenlang KE (2006) Importance of alternative food resources for browsing by roe deer on deciduous trees: the role of food availability and species quality. *For Ecol Manag* 226:248–255. <https://doi.org/10.1016/j.foreco.2006.01.045>
- Ohse B, Hammerbacher A, Seele C, Meldau S, Reichelt M, Ortman S, Wirth C (2017) Salivary cues: simulated roe deer browsing induces systemic changes in phytohormones and defence chemistry in wild-grown maple and beech saplings. *Funct Ecol* 31:340–349. <https://doi.org/10.1111/1365-2435.12717>
- Ohse B, Seele C, Holzwarth F, Wirth C (2017) Different facets of tree sapling diversity influence browsing intensity by deer dependent on spatial scale. *Ecol Evol* 7:6779–6789. <https://doi.org/10.1002/ece3.3217>
- Oom SP, Hester AJ, Elston DA, Legg CJ (2002) Spatial interaction models: from human geography to plant–herbivore interactions. *Oikos* 98:65–74. <https://doi.org/10.1034/j.1600-0706.2002.980107.x>
- Otway SJ, Hector A, Lawton JH (2005) Resource dilution effects on specialist insect herbivores in a grassland biodiversity experiment. *J Anim Ecol* 74:234–240. <https://doi.org/10.1111/j.1365-2656.2005.00913.x>
- Palmer SCF, Hester AJ, Elston DA, Gordon IJ, Hartley SE (2003) The perils of having tasty neighbors: grazing impacts of large herbivores at vegetation boundaries. *Ecology* 84:2877–2890. <https://doi.org/10.1890/02-0245>
- Pellissier F (2013) Early physiological responses of *Abies alba* and *Rubus fruticosus* to ungulate herbivory. *Plant Ecol* 214:127–138. <https://doi.org/10.1007/s11258-012-0151-0>
- Perea R, Gil L (2014) Shrubs facilitating seedling performance in ungulate-dominated systems: biotic versus abiotic mechanisms of plant facilitation. *Eur J For Res* 133:525–534. <https://doi.org/10.1007/s10342-014-0782-x>
- Pietrzykowski E, McArthur C, Fitzgerald H, Goodwin AN (2003) Influence of patch characteristics on browsing of tree seedlings by mammalian herbivores. *J Appl Ecol* 40:458–469. <https://doi.org/10.1046/j.1365-2664.2003.00809.x>
- R Core Team (2020) R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna. <http://www.R-project.org>
- Reimoser F, Gossow H (1996) Impact of ungulates on forest vegetation and its dependence on the silvicultural system. *For Ecol Manag* 88:107–119. [https://doi.org/10.1016/s0378-1127\(96\)03816-9](https://doi.org/10.1016/s0378-1127(96)03816-9)
- Root RB (1973) Organization of a Plant-Arthropod Association in simple and diverse habitats: the fauna of collards (*Brassica oleracea*). *Ecol Monogr* 43:95–124. <https://doi.org/10.2307/1942161>
- Rozenberger D, Mikac S, Anić I, Diaci J (2007) Gap regeneration patterns in relationship to light heterogeneity in two old-growth beech-fir forest reserves in South East Europe. *Forestry* 80:431–443. <https://doi.org/10.1093/forestry/cpm037>
- Schlather M, Ribeiro PJ Jr, Diggle PJ (2004) Detecting dependence between marks and locations of marked point processes. *J Roy Stat Soc Ser B (Stat Method)* 66:79–93. <https://doi.org/10.1046/j.1369-7412.2003.05343.x>
- Senft RL, Coughenour MB, Bailey DW, Rittenhouse LR, Sala OE, Swift DM (1987) Large herbivore foraging and ecological hierarchies. *Bioscience* 37:789–799. <https://doi.org/10.2307/1310545>
- Shimatani K (2002) Point processes for fine-scale spatial genetics and molecular ecology. *Biom J* 44:325–352. [https://doi.org/10.1002/1521-4036\(200204\)44:3%3c325::AID-BIMJ325%3e3.0.CO;2-B](https://doi.org/10.1002/1521-4036(200204)44:3%3c325::AID-BIMJ325%3e3.0.CO;2-B)
- Simončič T, Bončina A, Jarni K, Klopčič M (2019) Assessment of the long-term impact of deer on understory vegetation in mixed temperate forests. *J Veg Sci* 30:108–120. <https://doi.org/10.1111/jvs.12702>
- Storms D, Aubry P, Hamann JL, Said S, Fritz H, Saint-Andrieux C, Klein F (2008) Seasonal variation in diet composition and similarity of sympatric red deer *Cervus elaphus* and roe deer *Capreolus capreolus*. *Wildl Biol* 14:237–250. [https://doi.org/10.2981/0909-6396\(2008\)14\[237:svidca\]2.0.co;2](https://doi.org/10.2981/0909-6396(2008)14[237:svidca]2.0.co;2)
- Suchomel J, Heroldova M, Purchart L, Homolka M (2010) Herbivore impact on beech in selected tree plantations in the Beskydy and Jeseníky Mountains, vol 3. Mendel University in Brno, Beskydy, pp 187–192
- Tahvanainen JO, Root RB (1972) The influence of vegetational diversity on the population ecology of a specialized herbivore, *Phyllotreta cruciferae* (Coleoptera: Chrysomelidae). *Oecologia* 10:321–346. <https://doi.org/10.1007/BF00345736>
- Tsegai AT, Wang L, Wang DL, Huang Y, Lin HJ, Li J, Liu C (2013) Effects of spatial distribution on plant associational defense against herbivory. *Basic Appl Ecol* 14:680–686. <https://doi.org/10.1016/j.baae.2013.09.007>
- Underwood N, Inouye BD, Hämbäck PA (2014) A conceptual framework for associational effects: when do neighbours matter and how would we know? *Q Rev Biol* 89:1–19. <https://doi.org/10.1086/674991>
- Visscher DR, Merrill EH, Fortin D, Frair JL (2006) Estimating woody browse availability for ungulates at increasing snow depths. *For Ecol Manag* 222:348–354. <https://doi.org/10.1016/j.foreco.2005.10.035>
- Wang L, Wang DL, Bai YG, Jiang GT, Liu JS, Huang Y, Li YX (2010) Spatial distributions of multiple plant species affect herbivore foraging selectivity. *Oikos* 119:401–408. <https://doi.org/10.1111/j.1600-0706.2009.17774.x>
- Wiegand T, Moloney KA (2004) Rings, circles, and null-models for point pattern analysis in ecology. *Oikos* 104:209–229. <https://doi.org/10.1111/j.0030-1299.2004.12497.x>
- Wiegand T, Moloney KA (2014) Handbook of spatial point-pattern analysis in ecology, 1st edn. Chapman and Hall/CRC, Boca Raton
- Wiggins NL, McArthur C, Davies NW (2006) Diet switching in a generalist mammalian folivore: fundamental to maximising intake. *Oecologia* 147:650–657. <https://doi.org/10.1007/s00442-005-0305-z>
- Zambrano J, Fagan WF, Worthy SJ, Thompson J, Uriarte M, Zimmerman JK, Umana MN, Swenson NG (2019) Tree crown overlap improves predictions of the functional neighbourhood effects on tree survival and growth. *J Ecol* 107:887–900. <https://doi.org/10.1111/1365-2745.13075>
- Zollner PA, Lima SL (1999) Search strategies for landscape-level interpatch movements. *Ecology* 80:1019–1030. <https://doi.org/10.2307/177035>