Spatial patterns of living and dead small trees in subalpine Norway spruce forest reserves in Switzerland

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A B S T R A C T
Spatial patterns can reveal a lot about ecological processes, but our knowledge of the spatial ecology of tree regeneration at a fine scale is quite limited. Therefore, we studied the spatial patterns of living and dead small trees in two subalpine Norway spruce forest reserves in Switzerland (Scatlà and Bödmerenwald) using three types of analyses. First, we investigated the distances of small trees to the nearest large neighboring tree and, by using maximum distances as indicator, inferred the size of forest gaps, detecting mainly forest gaps of small size, although with two exceptions that were driven by large-scale disturbances. Second, we accounted for spatial inhomogeneity in the pattern of small and large trees (i.e., variations in local tree densities) by including environmental covariates in point pattern models. Latitude (within the forest reserve), elevation and aspect contributed significantly to explaining the density of living and dead small trees, and partly of living and dead large trees. Yet, the influence of these environmental covariates varied between the two reserves due to their different topography and peculiar site conditions. Third, we analyzed neighborhood interactions between small and large trees based on the vicinity and size of trees. In both forest reserves, small living trees were randomly dispersed around large dead trees over a broad range of distances and, at certain distances in one reserve, even dispersed away from them. Small living trees further showed clustering around large living trees at short distances and dispersion at large distances. Small dead trees featured mainly a random pattern, although with a tendency to cluster around large neighbors at short distances, irrespective whether these were living or dead. Yet, the weakening of clustering with increasing distances indicates that the influence of large trees on small trees varies with spatial scale and thus that these neighborhood interactions are scale-dependent. Overall, our study contributes to a better understanding of the spatial ecology of mortality in small trees and ultimately of tree regeneration processes and stand dynamics in mountain forests.

1. Introduction

Tree mortality, together with tree growth and regeneration, is a major driver of the development of forest ecosystems (Watt, 1947; Remmert, 1991; Zanini et al., 2006). For a comprehensive understanding of forest dynamics, a multitude of processes in the tree regeneration stage must be considered, including the vertical stratification and horizontal interactions that are of particular ecological significance. On the one hand, horizontal spatial patterns of forest structure that correspond to the distribution of trees in space are driven by spatial inhomogeneity, i.e. variations in local tree density, which may be explained partly by terrain characteristics such as elevation, aspect and slope (Pélissier and Goreaud, 2001). On the other hand, spatial patterns are determined by neighborhood interactions between forest trees over a range of spatial scales, which usually strengthen with increasing proximity of trees (Kenkel, 1988), making the identification of influential neighboring trees crucial (Zenner and Peck, 2018). These neighborhood interactions can be both positive or negative, with facilitation among tree individuals counteracting competition for resources and environmental stress (Liu et al., 2020). For instance, facilitation occurs when early-stage light-demanding species facilitate the recruitment of late-stage shade-tolerant species (Zanini et al., 2006).

The spatial patterns of forest trees are commonly investigated using point pattern analyses (Ripley, 1977; Dale, 1999; Fortin and Dale, 2005;
Brown et al., 2016), with a particular focus on whether trees are randomly distributed, clustered or dispersed as well as on whether neighborhood interactions between trees are positive, negative or missing (i.e., second-order statistics such as Ripley’s K function, Illian et al., 2008). Past point pattern analyses on forest trees have investigated neighborhood interactions (1) between living and dead trees, (2) among trees of different sizes, with large trees having strongly asymmetric effects on smaller trees (Turner andFranz, 1986), (3) across study sites with different climatic conditions (e.g., Zenner, 2000; LeMay and Temesgen, 2005; Pomerening et al., 2012; Pomerening and Granbark, 2019), and (4) over different sizes of forest gaps resulting from large-scale disturbances (e.g., Svoboda et al., 2010).

Previous research has shown, for instance, that small conifer trees in dry regions tend to cluster in moist microsites (Simon et al., 2019) and around large living trees (LeMay et al., 2009), while under moister conditions they are found at larger distances from large living trees. Competition in the self-thinning stage (Oliver and Larson, 1996) was found to result in the clustering of dead conifer trees, while living trees were distributed randomly (Kienkol, 1986). Competitive mortality decreases as trees become larger (Getzin et al., 2006), and therefore the spatial pattern of large dead trees is more likely to be driven by disturbances as well as by abiotic and biotic factors occurring locally and affecting adjacent trees (Larson and Churchill, 2008). For example, stand-scale windstorms or local tree falls followed by insect infestations or infections by fungal pathogens are likely to lead to a clustered pattern (Dobbertin et al., 2001; Kelly and Meentemeyer, 2002; Liu et al., 2007; Stadelmann et al., 2014).

Local tree densities typically vary in response to topographical characteristics such as longitude, latitude, elevation and aspect and to other environmental influences such as temperature, precipitation and soil features. However, there is still little known about the influence of topographical and environmental covariates on local tree densities (Zenner and Hibbs, 2000; Larson and Churchill, 2012; Velázquez et al., 2016), in spite of the existence of suitable methods (i.e., first-order statistics such as the intensity and point density functions, Illian et al., 2008) to include these covariates in the models so as to capture terrain characteristics and, ultimately, account for spatial inhomogeneity.

Spatial inhomogeneity and neighborhood interactions can be combined using recently developed multitype point pattern analysis, which describes the spatial pattern of processes yielding more than one type of points (Särkkä and Renshaw, 2006; Pomerening et al., 2011; Robertson and Roberts, 2013). Combining spatial inhomogeneity and neighborhood interactions allows for detecting relationships between topography and neighboring trees over a range of spatial scales. Lastly, the spatial patterns of living and dead small trees (i.e., trees with a stem diameter at breast height (hereafter ‘dbh’) < 10 cm; our convention) are still poorly understood, but could be studied using multitype point patterns that account for spatial inhomogeneity and neighborhood interactions.

A particularly interesting case study to apply multitype point pattern analysis are subalpine Norway spruce (Picea abies L.) forests reserves, because (1) their monitoring provides valuable data to study spatial patterns of natural tree regeneration without being affected by human intervention; and (2) they combine strong spatial inhomogeneity via large gradients of topography and environmental variables such as temperature, precipitation and snow cover. Competition for resources occurs not only between small trees and understory herbaceous vegetation, but also among neighboring tree regeneration, especially in forest gaps (Gray and Spies, 1997; Kothke and Bruelheide, 2010). Moreover, the abundance and success of tree regeneration in subalpine Norway spruce forests typically decreases with increasing elevation, and tree height and radial growth also tend to decrease along the elevational gradient (Li et al., 2003).

We conducted a comprehensive spatial analysis in two subalpine Norway spruce forest reserves by analyzing four spatial patterns based on tree size and status, i.e. small and large trees combined with living and dead trees. Here, we (i) investigated nearest neighbor distances between small and large trees and thus inferred the size of forest gaps, as we expected tree regeneration to be more abundant in large gaps than in small gaps; (ii) accounted for spatial inhomogeneity and thus explained variations in local tree densities, expecting the influences of environmental covariates to vary between the forests due to large environmental gradients and different topography; and (iii) analyzed neighborhood interactions with a focus on the effect of large living and dead neighboring trees on the spatial pattern of living and dead small trees. Given the pronounced small-scale variation in topography in subalpine forests, we expected small trees to be clustered around large neighboring trees in the few suitable microsites for tree growth and survival, as well as a shift from clustering towards dispersion with increasing distance from the large trees and suitable microsites, respectively. Specifically, we addressed the following research questions:

1) What is the range of distances of small living and dead trees from large living and dead trees, and what can be inferred from this regarding the size of gaps?
2) How does the influence of the environmental covariates on the local density of tree regeneration vary between forest reserves?
3) How do neighborhood interactions between living and dead small and large trees vary with distance?

2. Methods

2.1. Study sites

We selected two strictly protected forest reserves in the subalpine zone of Switzerland: Scatlé and Bödmerenwald, which are part of the Swiss Forest Reserves Network (Hobi et al., 2020; Mathys et al., 2021). Both reserves are almost pure Norway spruce forests in a near-natural state, and hence they are particularly suitable to investigate natural processes of forest dynamics.

The core area of the reserve of Scatlé that we used here covers 3.47 ha (permanent plot #1, selected for its comparability in area and number of trees with the permanent plots of the reserve of Bödmerenwald) and its penultimate and last inventories occurred in 2006 and 2018, respectively. The core area of the reserve of Bödmerenwald covers 4.87 ha (four permanent plots) and its penultimate and last inventories occurred in 2003 and 2018, respectively. In both reserves, no human intervention occurred since their protection (Brang et al., 2011). Scatlé is a talus forest with silicate (verrucano) bedrock located between 1510 and 2015 m a.s.l. on a steep (60% slope steepness) east- to northeast-facing slope in the Canton of Grisons, in the Swiss Central Alps (coordinates: 46°47’N 9°03’E). This reserve is characterized by a semi-continental climate (i.e., large fluctuations in daily and seasonal temperature and moderate precipitation), with 2.2 °C mean annual temperature and 1440 mm annual precipitation. Bödmerenwald is a karst forest with limestone as bedrock located between 1400 and 1702 m a.s.l. on a less steep (35% slope steepness) west-facing slope in the Canton of Schwyz, in the northern Swiss Pre-Alps (coordinates: 46°59’N 8°51’E). This reserve is experiencing a highly oceanic climate (i.e., lower temperature fluctuations and higher precipitation compared to Scatlé), with 3–4 °C mean annual temperature and >2500 mm annual precipitation.

2.2. Datasets

In the last survey of 2018, the dataset of permanent plot #1 in Scatlé included 1888 living and dead trees, and in Bödmerenwald 1422 living and dead trees (in both reserves, dbh ≥ 4 cm). Almost all trees were Norway spruce, with 6 exceptions in Scatlé (rowan and red elderberry) and 10 in Bödmerenwald (rowan, beech and sycamore).

The coordinates of all living and standing dead trees had been
recorded with decimeter precision during the last survey in each reserve. In the field, the coordinates of the trees were recorded in a local coordinate system, measuring the horizontal distances from a reference point with a Vertex and the angles with a compass on a tripod. Afterwards, the local coordinates were georeferenced, so that the trees of both reserves had the same coordinate system. For each tree, additional information such as status (whether it was living or dead), dbh, height, and species was collected. To analyze the spatial patterns through neighborhood interactions based on tree status and size, we grouped living trees vs. dead trees and used a dbh threshold of 10 cm, which lies just below the threshold of the thicket stage, to distinguish between ‘small’ and ‘large’ trees, leading to the following four groups (Table 1): in Scatè, there were 448 small living trees (23.3% of the total trees), 1293 large living trees (67.1%), 83 small dead trees (4.3%) and 64 large dead trees (3.3%). In Bödmerenwald, there were 210 small living trees (14.8%), 1133 large living trees (79.7%), 13 small dead trees (0.9%) and 66 large dead trees (4.6%). The fraction of dead trees in total was somewhat lower in Scatè, amounting to 7.8% (n = 147) compared to 5.6% (n = 79) in Bödmerenwald (Table 1). The dbh distributions of the living and dead trees were left-skewed in Scatè, while they were more uniform in Bödmerenwald (Fig. 1).

To represent the spatial inhomogeneity of tree density that results from the variability in topography, we used longitude (x-coordinates), latitude (y-coordinates), elevation (z-coordinates) and aspect with an accuracy of 0.5 m. This topographical information was derived from an extremely precise digital terrain model of Switzerland (swissALTI3D from swisstopo). Aspect was transformed into two gradients: northness = \(\cos(\text{aspect}/360 \times 2\pi)\), with north = 1 and south = −1; and eastness = \(\sin(\text{aspect}/360 \times 2\pi)\), with east = 1 and west = −1. This topographical information was stored as pixel images, with values for each grid point in a rectangular grid inside the observation window (i.e., forest reserve), and was used as covariates (i.e. ‘explanatory’ variables) with continuous numerical values in the statistical analysis (Baddeley et al., 2012). Although slope steepness is quite different between the two forest reserves (average of 60% in Scatè vs. 35% in Bödmerenwald), the variation within each forest was of minor extent, and therefore we did not include this variable in the set of covariates.

### 2.3. Statistical analyses

We grouped the trees by considering tree status (living or dead) as well as tree size (small or large). This information was attached as marks to the points that thus classify the points into several types. Based on these marks, we generated four bivariate multitype point patterns: (1) small living trees around large living trees; (2) small living trees around large dead trees; (3) small dead trees around large living trees; and (4) small dead trees around large dead trees, whereby our reference mark was always the small trees (either living or dead). Then, we statistically analyzed these four multitype point patterns by focusing on three types of analyses: nearest neighbor-based analysis, distance-based analysis, and analysis based on Ripley’s L function. All analyses were performed in the R software for statistical computation (R Core Team, 2020).

The first analysis considered the nearest neighbor of each tree only, because usually the effect of a neighboring tree is stronger between trees close to one another (Tobler, 1970). To this end, we calculated nearest neighbor distances within the four bivariate multitype point patterns, i.e. the distance of each small tree to the next large tree, using the function “nncross” of the “spatstat” package in the R software, assuming that the spatial pattern of trees depends on the interactions among them.

Since a tree is typically affected by more than one single neighboring tree, the number of neighbors per unit area (i.e. tree density) is a suitable indicator of the spatial pattern of trees, which can be spatially homogeneous or inhomogeneous. Under conditions of spatial homogeneity, tree density remains constant over space (Illian et al., 2008), i.e. a tree does have an equal probability of being at any position, and the tree positions are independent. The point pattern of such independent tree positions can be described by a homogeneous Poisson distribution and fulfills the assumptions of complete spatial randomness (CSR, Wiegand and Moloney, 2013). However, CSR is rare in natural forests, so the spatial inhomogeneity is usually described by an inhomogeneous Poisson distribution where tree density varies in response to some causal variables (first-order effect) and/or as a result of interactions between trees (second-order effect). These effects can lead to a positive clustering, or a negative association (dispersion, repulsion) among trees.

Therefore, in the second analysis we considered all neighbors within a varying distance and accounted for the spatial inhomogeneity of the tree pattern in Scatè and Bödmerenwald using environmental covariates (coordinates and topographical information) as first-order effects. We further used tree status and tree size as second-order effects to generate multitype point patterns. For this distance-based analysis, we modeled local tree densities as a pattern with an inhomogeneous Poisson distribution (Baddeley et al., 2015). This required (a) a two-dimensional observation window representing the perimeter of the forest reserves, (b) the position of trees (i.e., the spatial location of a set of points) and their marks (see above), and (c) environmental covariates (see above), assuming that the spatial pattern of trees depends on the topology of the forest reserves. This allows for covariate effects on the intensity (i.e., average density of trees). Because the models did not converge without standardization of the variables, the covariates were transformed to a mean of 0 and a variance of 1, as centering and scaling facilitate model convergence and allow for the comparison of effect sizes (Fletcher and Fortin, 2018).

For the four bivariate multitype point patterns, we fitted the following model using the function “ppm” of the “spatstat” R package:

\[
\log(\lambda(u, m)) = \alpha_0 + \alpha_m + \beta_{\text{int}}C_1(u) + \cdots + \beta_{\text{int}}C_r(u)
\]

where \(\lambda(u, m)\) is the intensity function for trees of type \(m\) at location \(u\) that is modelled using a log link, with different intercepts \(\alpha\) for each mark \(m\) (i.e., different intensity for each tree type) and different slopes \(\beta\) for each mark \(m\) (i.e., different spatial trend for each tree type). The slopes \(\beta_1, \ldots, \beta_r\) vary with the covariates \(C_1, \ldots, C_r\), where \(C(u)\) represents the values of the covariates at location \(u\). The fitted coefficient \(\alpha_0\) is the intercept for small (either living or dead) trees. We handled the categorical mark as treatment contrast, where the first level of the mark \(m\) corresponds to the reference level, which in our study always refers to the small (either living or dead) trees, whereas the second level of the mark \(m\) is always the large trees, either living or dead. Therefore, the fitted coefficient \(\alpha_m\) is the intercept of small (either or dead) trees, whereas \(\alpha_{\text{int}}\) is the difference in the intercept between large and small (either living or dead) trees.

In the third analysis, we assessed whether the four bivariate multitype point patterns were clustered, random or dispersed, by calculating and visualizing Ripley’s inhomogeneous bivariate L function (Baddeley et al., 2000; Dixon, 2002; Møller and Waagepetersen, 2003), which is the linear transformation of Ripley’s inhomogeneous bivariate K function (Loosmore and Ford, 2006), so that its expected value for a random point pattern is 0, with \(L_{\text{small}}(r) > r\) indicating clustering while \(L_{\text{small}}\)
large(r) < r indicates dispersion of the multitype point pattern. Again, the bivariate L function was applied to the four combinations of point patterns, i.e. L_{small living, large living}, L_{small living, large dead}, L_{small dead, large living}, and L_{small dead, large dead}. The L function was corrected with the “border” method in the function “Lcross.inhom” of the “spatstat” R package, v1.63-3 (Baddeley and Turner, 2005) to take into account edge effects (Ripley, 1988; Baddeley, 1998; Goreaud and Pelissier, 1999; Pommernening and Stoyan, 2006), i.e. the bias for the non-observability of trees outside the observation window, leading to trees close to the borders of the observation window having larger nearest neighbor distances and fewer neighbors, respectively.

3. Results

3.1. Nearest neighbor analyses

3.1.1. Scatle

In Scatle, the average and maximum distances (i.e., indicator of gap size) of small living trees to the nearest large living tree were 1.7 m and 13.1 m, respectively, while those to the nearest large dead tree were 12.4 m and 31.3 m (Fig. 2A and B, Fig. 3A and B). Small dead trees were on average 1.3 m and a maximum of 4.4 m away from the next large living neighbor tree, while the average distance was 9.8 m and the maximum distance was 25.6 m from the next large dead neighbor (Fig. 2C and D, Fig. 3C and D).

3.1.2. Bödmerenwald

In Bödmerenwald, the average and maximum distances of small living trees to the nearest large living tree were 3.5 m and 12.6 m, respectively, while those to the nearest large dead tree were 20.5 m and 80.1 m (Fig. 4A and B, Fig. 5A and B). Small dead trees were on average 1.0 m and a maximum of 2.7 m away from the next large living neighbor, while the average distance was 11.7 m and the maximum distance was 24.1 m from the next large dead neighbor (Fig. 4C and D, Fig. 5C and D).
3.2. Spatial inhomogeneity

3.2.1. Scatle

**Pattern A: Small living around large living trees** – In Scatle, the local density of small living trees decreased with increasing latitude, i.e. the number of small living trees was larger in the southern part of the reserve (estimate of latitude = −1.22, \( P < 0.001 \), Table 2, Fig. 3A). Aspect also had a significant negative effect on the local density of small living trees: the more the terrain was north- and west-facing, the more small living trees grew there (estimates of northness = 0.28 and of eastness = −0.21, \( P < 0.05 \) and \(< 0.001 \), respectively). Large living trees (contrast) had a higher local density than small living trees (reference level; estimate of marks: large.living = 1.66, \( P < 0.001 \)). Furthermore, the decrease of the local density of large living trees with increasing latitude was significantly smaller than for small living trees (estimate of interaction = 0.74, \( P < 0.001 \)). Compared to small living trees, the local density of large living trees decreased significantly the more the terrain was north-facing (estimate of interaction = −0.37, \( P < 0.01 \)).

**Pattern B: Small living around large dead trees** – The local density of small living trees around large dead individuals coincided with that around large living individuals (pattern A). The local density of small living trees decreased significantly with increasing latitude (estimate = −1.21, \( P < 0.001 \), Table 2, Fig. 3B) and eastness (estimate = −0.23, \( P < 0.001 \)), but increased with increasing northness (estimate = 0.27, \( P < 0.05 \)). In contrast to pattern A, large dead trees had a significantly lower local density than small dead trees (estimate of marks: large.dead = −1.31, \( P < 0.001 \)). The increase of the local density of large dead trees with increasing latitude was significantly higher than that of small living trees (estimate of interaction = 0.86, \( P < 0.001 \)).

**Pattern C: Small dead around large living trees** – As in patterns A and B for the living small trees, the local density of small dead trees also decreased significantly with increasing latitude (estimate = −2.32, \( P < 0.001 \), Table 2, Fig. 3C). In addition, it decreased significantly with increasing elevation (estimate = −2.09, \( P < 0.05 \)). Aspect had no
significant influence on the local density of small dead trees. As in pattern A, the local density of large dead trees was significantly higher than that of the small living trees (estimate of marks: large.living = 4.40, $P < 0.001$, Table 2). The local density of large living trees decreased with increasing latitude significantly less than that of small dead trees (estimate of interaction $= 1.85$, $P < 0.001$). Compared to small dead trees, the local density of large living trees increased with longitude and elevation (estimates of interaction $= 2.69$ and 2.34, respectively, $P < 0.05$ for both).

**Pattern D: Small dead around large dead trees** – The local density of small dead trees around large dead individuals coincided with that around large living individuals (pattern C). The local density of small dead trees decreased significantly with increasing latitude (estimate $= -2.25$, $P < 0.001$, Table 2, Fig. 3D). Again, elevation and aspect had no significant influence on the local density of small dead trees. As in pattern A and C, large dead trees had a significantly higher local density than small living trees (estimate of marks: large.dead $= 1.40$, $P < 0.001$, Table 3). The local density of large dead trees decreased with increasing latitude significantly less than that of small trees (estimate of interaction $= 1.92$, $P < 0.001$).

### 3.2.2. Böderenwald

**Pattern A: Small living around large living trees** – In Böderenwald, the local density of small living trees increased significantly with increasing latitude (estimate $= 1.37$, $P < 0.001$, Table 3, Fig. 5A) and elevation (estimate $= 1.06$, $P < 0.001$). Aspect partly influenced the local density of small living trees, but only northness had a significant negative effect (estimate $= -0.27$, $P < 0.001$). Large living trees had a significantly higher local density than small living trees (estimate of marks: large.living $= 1.98$, $P < 0.001$). In significant contrast to and with opposite sign compared to that of small living trees (reference level), the local density of large living trees decreased significantly with increasing latitude (estimate of interaction $= -1.49$, $P < 0.001$). Compared to small living trees (reference level), the local density of large living trees increased with elevation (estimate of interaction $= -0.99$, $P < 0.001$) and decreased with northness (estimate interaction $= 0.17$, $P < 0.05$) significantly less.

**Pattern C: Small dead around large living trees** – The local density of small living trees around large dead individuals coincided with that around large living trees (pattern A). The local density of small trees increased significantly with increasing latitude (estimate $= 1.35$, $P < 0.001$, Table 3, Fig. 5B) and elevation (estimate $= 1.05$, $P < 0.001$) as well as with decreasing northness (estimate $= -0.25$, $P < 0.01$). In contrast to pattern A, large dead trees had a significantly lower local density than small living trees (estimate of marks: large.dead $= -0.90$, $P < 0.001$). In significant contrast to and with opposite sign compared to that of small living trees (reference level), the local density of large dead trees decreased with increasing latitude (estimate of interaction $= -1.85$, $P < 0.001$) and elevation (estimate of interaction $= -1.21$, $P < 0.001$).

**Pattern B: Small living around large dead trees** – The local density of small living trees around large dead individuals coincided with that around large dead trees (pattern D). The local density of small living trees increased significantly with increasing latitude (estimate $= -1.52$, $P < 0.05$, Table 3, Fig. 5C). As in pattern A, the local density of large living trees was higher than that of small dead trees (estimate of marks: large.living $= 5.98$, $P < 0.001$). The influence of topography and environmental covariates on the local density of large
living trees did not vary significantly from that on the local density of small dead trees (reference level).

**Pattern D: Small dead around large dead trees** – In line with pattern C, latitude had a significant negative effect on the local density of small dead trees (estimate $= -1.66$, $P < 0.01$, Table 3, Fig. 5D). As in pattern A and C, the local density of large dead trees was higher than that of small dead trees (estimate of marks: large.dead $= 3.20$, $P < 0.01$). As for pattern C, no significant difference was observed between the influence of topography and environmental covariates on the local density of small and large dead trees.

### 3.3. Neighborhood interactions

#### 3.3.1. Scatle

**Pattern A: Small living around large living trees** – The model indicated significant neighborhood interactions between neighboring trees, with clustering of the small living trees around large living trees at a radius below 9.3 m and again from 14.0 m to 15.9 m, and dispersion at a radius above 24.6 m (Fig. 6A).

**Pattern B: Small living around large dead trees** – The model indicated no neighborhood interactions between neighboring trees, with a random pattern for small living trees around large dead trees within a radius of up to 50 m (Fig. 6B).

**Pattern C: Small dead around large living trees** – The model indicated a tendency of small dead trees to cluster around large living trees at radii below 1.6 m, to feature a random pattern at radii between 1.6 and 40.5 m and significant dispersion above 40.5 m (Fig. 6C).

**Pattern D: Small dead around large dead trees** – The model indicated a tendency of small dead trees to cluster around large dead trees at radii below 1.9 m, significant clustering of small dead trees around large dead trees only at a radius between 29.6 and 35.4 m, and otherwise a random pattern (Fig. 6D).
3.3.2. Bödmerenwald

Pattern A: Small living around large living trees – The model indicated significant neighborhood interactions between neighboring trees, with clustering of small living trees at a radius below 5.6 m and dispersion at a radius above 10.7 m (Fig. 7A).

Pattern B: Small living around large dead trees – The model indicated significant neighborhood interactions between neighboring trees, with a tendency of small living trees to cluster around large dead trees at radii below 1.8 m and dispersion at radii of 6.7–31.0 m and larger than 36.5 m (Fig. 7B).

Pattern C: Small dead around large living trees – The model showed no significant neighborhood interactions between neighboring trees, with solely a tendency of small dead trees to cluster around large living trees at radii below 2 m and a random pattern up to a radius of 30 m (Fig. 7C).

Pattern D: Small dead around large dead trees – The model indicated significant neighborhood interactions between neighboring trees, with clustering of small dead trees around large dead trees at radii of 2.4–3.2 m and a tendency to cluster at radii below 2.4 m, while at radii above 3.2 m they showed a random pattern (Fig. 7D). Since the number of small dead trees was quite low in Bödmerenwald, the models did not fit well the spatial patterns C and D, and therefore the accuracy of these latter two marked point pattern analyses is limited.

4. Discussion

In line with our hypotheses, we found short distances between small trees and the nearest large tree, thus revealing the presence of predominantly small forest gaps. Our findings further highlight how the influence of the environmental covariates explaining the spatial inhomogeneity varies between the two reserves. Lastly, we found significant interactions between small and large trees, as discussed below.

4.1. Forest gaps in subalpine forest reserves

In both subalpine Norway spruce forest reserves, only few large forest gaps occurred (gap sizes of approximately 50 m × 50 m), but living and dead small trees showed rather short maximum distances to the nearest large living tree, indicating the predominance of small forest gaps. These gaps are commonly formed by the death of single large trees initiated by local wind impacts, fungal infections, and small-scale insect infestations (e.g., Kneeshaw and Bergeron, 1998; Peck et al., 2014; Zenner et al., 2015). In contrast, larger gaps typically arise from large-scale disturbances such as snow avalanches or windthrows (Svoboda et al., 2010), which is in line with our findings: the large gap observed in the southern part of Scatle was caused by an avalanche that occurred for the last time in the winter of 1983/1984 (Amt für Wald und Naturgefahren Canton of Grisons, 2019), while the large gap observed in the northern part of Bödmerenwald was caused by the storm Vivian in 1990 (Liechti et al., 2005). Windthrows occur often in Norway spruce forests that are exposed to the main wind direction (Usbeck et al., 2012), and westerners are blowing nearly constantly in this west-facing forest reserve (Frey and Bichsel, 2001). Both large-scale disturbances created suitable conditions for tree regeneration, with a new tree generation growing abundantly in the large forest gaps (Fig. 4A and B, Fig. 5A and B), which is in line with results of past studies on Norway spruce (Wild et al., 2014). The high density of tree regeneration in large forest gaps
reflects the light and warmth requirements of tree regeneration (Brang, 1998; Holtmeier, 2009) and has been reported earlier (Wolf, 2005; Liu et al., 2020). Although lying dead trees were not considered in our analyses, it is clear that large-scale disturbances such as avalanches and windthrows lead to large amounts of lying coarse deadwood, which are a highly suitable substrate for spruce regeneration in subalpine forests (Wohlgemuth and Kramer, 2015).

4.2. Spatial inhomogeneity

Longitude, latitude, elevation and aspect (northness and eastness) that represent environmental covariates in the point pattern analyses contributed to explaining spatial inhomogeneity, i.e. variation in local tree densities. In general, the influence of the environmental covariates on the local density of small living trees around large living individuals was consistent with that of those around large dead trees, and the same applied to the local density of small dead trees. Moreover, the local density of large trees was influenced partly by the same environmental covariates as that of small trees. This consistency was found in both forest reserves and indicates that the spatial inhomogeneity explained through topography is independent of whether the small trees are located around large living or large dead trees. The only exception was the effect of elevation in Scatle, which was significant for small dead trees around large living trees but not around dead trees. The environmental covariates had similar effects on the local density of both living and dead large trees, which may be due to the slow regeneration dynamics in the subalpine zone. Specifically, the large trees may have died and died large trees, which may be due to the slow regeneration dynamics in the subalpine zone.

<table>
<thead>
<tr>
<th>Pattern</th>
<th>Model</th>
<th>Covariate</th>
<th>Estimate</th>
<th>S.E.</th>
<th>CI95.lo</th>
<th>CI95.hi</th>
<th>Z-value</th>
<th>Z-test</th>
</tr>
</thead>
<tbody>
<tr>
<td>A</td>
<td>Small living Trees around</td>
<td>latitude</td>
<td>-1.22</td>
<td>0.10</td>
<td>-1.42</td>
<td>-1.01</td>
<td>4.89</td>
<td>11.76</td>
</tr>
<tr>
<td>A</td>
<td>Small living Trees around</td>
<td>elevation</td>
<td>-0.13</td>
<td>0.42</td>
<td>-0.95</td>
<td>0.69</td>
<td>-0.32</td>
<td>4.83</td>
</tr>
<tr>
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<td>Small living Trees around</td>
<td>northness</td>
<td>0.28</td>
<td>0.13</td>
<td>0.02</td>
<td>0.54</td>
<td>2.13</td>
<td>4.94</td>
</tr>
<tr>
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<td>eastness</td>
<td>-0.21</td>
<td>0.06</td>
<td>-0.33</td>
<td>-0.09</td>
<td>5.12</td>
<td>11.76</td>
</tr>
<tr>
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<td>marks:large.living</td>
<td>1.66</td>
<td>0.10</td>
<td>1.46</td>
<td>1.86</td>
<td>22.56</td>
<td>11.76</td>
</tr>
<tr>
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<td>large.living:longitude</td>
<td>0.38</td>
<td>0.59</td>
<td>-0.78</td>
<td>1.54</td>
<td>5.12</td>
<td>11.76</td>
</tr>
<tr>
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<td>Large dead trees</td>
<td>large.living:latitude</td>
<td>0.74</td>
<td>0.11</td>
<td>0.52</td>
<td>0.96</td>
<td>11.76</td>
<td></td>
</tr>
<tr>
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<td>large.living:elevation</td>
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<tr>
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<td>0.14</td>
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<td>-0.11</td>
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<tr>
<td>A</td>
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<td>-0.05</td>
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<td>5.12</td>
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</tr>
</tbody>
</table>

Note: reference marks are always small trees, either living or dead. Mean and standard deviation of the unscaled covariates are: 9° 25.65’ ± 2.02’ for latitude, 1638.7 ± 30.2 m a.s.l. for elevation, 87.1° ± 24.5° for aspect.

Table 2
Model output of the forest reserve of Scatle for each of the four inhomogeneous multitype Poisson patterns using longitude (x-coordinates), latitude (y-coordinates), elevation (z-coordinates), northness and eastness (aspect) and marks as well as their interactions (due to the different slopes β for each mark m) as covariates. Values and symbols are estimates (Eq. (1)), standard errors of the estimates (S.E.), lower and upper 95% confidence limits for the estimates (CI95.lo and CI95.hi, respectively), Z-values (i.e., significance of the effects tested using Z-tests). Asterisks indicate the significance level of the Z-tests: ***, <0.001, **, <0.01, *, <0.05.
As expected, the environmental covariates used to represent topography contributed significantly to explaining the spatial inhomogeneity of small trees. First, the density of living small trees around large trees, irrespective of whether these were living or dead, decreased significantly in Scatle with increasing latitude (cf. the avalanche in the southern part mentioned above) and eastness, as well as with decreasing northiness. Yet, eastness was less significant than latitude. Second, the density of small living trees in Bödmerenwald was significantly influenced by latitude, but positively in contrast to Scatle (cf. windthrow in the northern part mentioned above). The density of living small trees in Bödmerenwald increased significantly with decreasing northiness, while eastness had no significance, and with increasing elevation. This last finding appears to be counter-intuitive, as the literature suggests a decreasing abundance of regeneration with increasing elevation (Batilori et al., 2010; Munoz Mazon et al., 2020), due to the declining production of viable seeds and decreasing seedbed quality (Körner, 2012). However, this decrease in the abundance of regeneration is typical of large elevation gradients, much larger than those found within the forest reserve of Bödmerenwald.

Lastly, the density of small dead trees was significantly and negatively influenced by latitude in both reserves and generally by fewer environmental covariates (i.e., only by latitude) than that of small living trees, suggesting that the spatial pattern of dead regeneration is not mainly driven by topography and thus spatial inhomogeneity plays a minor role for the mortality of tree regeneration compared to neighboring interactions. To the best of our knowledge, this finding has not been reported in the literature yet.

While latitude and northness had a significant influence in both reserves, although with opposite signs, the different topography in Scatle and Bödmerenwald led to differences of the spatial patterns of small
living trees between the two reserves, with eastness being significant in Scatìle, and elevation being significant in Bödmerenwald. Yet, these two covariates are relatively constant within each reserve (i.e., Scatìle is located on an east-facing slope and Bödmerenwald features a relatively small elevational gradient), which suggests that the variability at very small spatial scales, at the level of microsites, has possibly more ecological implications than the range of elevations or aspects within the reserves. Fortunately, we were able to capture this small-scale variability owing to the very high-precision digital terrain model. The small-scale variability is salient in both reserves and reflects their peculiar site conditions. Since Scatìle and Bödmerenwald are located on a talus and karst slope, respectively, the presence of large boulders and elongated ridges, respectively, causes strong terrain variations at very small spatial scales. In line with suitable microsites for Norway spruce regeneration observed in other subalpine forests (Baier et al., 2007), trees tend in both reserves to grow on mounds (i.e. elevated, convex microsites), which, compared to depressions (i.e. concave microsites), offer the advantages of early snowmelt as well as of low snow accumulation, a decreased risk of snow fungi infestation and reduced mechanical snow damage (Ott et al., 1997; Barbeito et al., 2012; Pröll et al., 2015), but at the same time feature the disadvantage of water limitation in the soil (Simon et al., 2011). Low soil moisture on mounds is an issue particularly directly around large trees, due to high water uptake and interception through the extensive superficial root system of Norway spruce (Puhe, 2003) on the one hand, and to snow interception and sublimation on branches of large trees (Pomeroy et al., 1998) on the other hand.

4.3. Neighborhood interactions

With Ripley’s inhomogeneous bivariate L function, we were able to...
assess and visualize the neighborhood interactions. Overall, the interactions between small and large trees were significant in both forest reserves, with large neighboring trees having a negative effect on small trees in pattern B only (cf. next paragraph), while a positive effect occurred in the other three patterns A, C and D (cf. subsequent paragraphs).

In Scatle, small living trees were distributed randomly around large dead trees irrespective of the radius (Fig. 6B), while in Bödmerenwald the random pattern shifted even towards dispersion at intermediate and large radii (Fig. 7B). In Bödmerenwald, we further observed a tendency of small living trees to cluster around large dead trees at very short radii (Fig. 7B), where they are most likely able to benefit from reduced competition for light after the death of the large trees, which reflects the classical “gap filling” dynamics (Yamamoto, 2000).

Small living trees in both forest reserves clustered around large living trees at short radii, but were dispersed at larger distances (Fig. 6A and Fig. 7A), which is in line with recent findings on Norway spruce in unmanaged forests (Janík et al., 2016). The observed decreasing clustering with increasing distance corresponds to expectations, but yet it is unlikely due to the hypothesized intensity of competition and facilitation decreasing with increasing distance from the large canopy trees, as suggested by Carrer et al. (2013). Small living trees are not particularly affected by light limitation through shading of large individuals in these subalpine, fairly open forest stands, but they rather profit from the same microsite conditions that were conducive to the establishment of the now large trees (Grubb, 1977). This reflects the fact that there are fewer favorable microsites with increasing distance that would allow for successful establishment. The observed clustering further implies that locations without large living trees are not suitable for small living trees probably due to adverse microsite conditions, even if they feature high
light availability (Canham et al., 1990). These unfavorable locations for both adult and small trees possibly correspond to depressions, while the elevated position on mounds is advantageous because of multiple factors, among others early snowmelt and reduced snow accumulation (Musselman et al., 2008; Renard et al., 2016), with consequent reduced susceptibility to infestation by cryophilic fungi (Barbetto et al., 2013). Snow load is a particularly strong factor in Bödmerenwald, where the climate is oceanic, but also in Scatle, even though there a more continental climate prevails.

Small dead trees showed a tendency to cluster around large trees at very short radii in both reserves, irrespective of whether the large trees were living or dead (Fig. 6C and D as well as Fig. 7C and D). The tendency of small dead trees to cluster around large living individuals at very short radii may arise from the dbh threshold for tree size (10 cm), since small dead trees typically show reduced radial growth rates starting several years prior to death (Bianchi et al., 2021) and thus tend to feature a smaller diameter than the surviving individuals of the same age. In the absence of human interventions and interspecific competition (note that 99.5% of the trees were Norway spruce), the tendency of small dead trees to cluster around large living individuals could therefore be driven by intraspecific competition within a single cohort. This form of competition, also known as conspecific self-thinning, often explains density effects in forests (Pommerening and Sánchez Meador, 2018), as recently reported for small trees (Piao et al., 2013; Yılmaz et al., 2019) and proposed for primary and old-growth forests (Hurst et al., 2012; Després et al., 2017).

4.4. Further aspects influencing spatial patterns of small living and dead trees

The present study does not include information on the causes of timing of tree death, which can be ascribed to a multitude of abiotic and biotic factors and often a combination of them (Manion, 1981; Das et al., 2011; Pommerening and Sárlká, 2013; Synek et al., 2020). Moreover, the multitude of abiotic and biotic mortality factors only partially explains the spatial pattern of dead trees, since the mortality events that we analyzed are constrained to occur only within the locations where tree regeneration was successfully reaching the caliperizing threshold of 4 cm dbh (Aakala et al., 2012). It is thus important to disentangle the effect of the mortality events from that of the initial spatial pattern of trees, which however evolves over time as trees become older and a large fraction of them die (Kint, 2005; Szmyt and Tarasius, 2018). Including the causes of tree death and repeating the point pattern analyses for tree sizes below the caliperizing threshold and across subsequent inventories would therefore strongly enhance our understanding of the spatial pattern of living and dead tree regeneration as well as its change over time (Hurst et al., 2011; Ramage et al., 2017).

5. Conclusion

We investigated the spatial patterns of living and dead small trees in two subalpine uneven-aged and unmanaged Norway spruce forests in Switzerland using three types of analysis.

(1) Using a nearest neighbor analysis, we found small distances of small individuals to the next neighboring large tree in both forest reserves, revealing predominantly small forest gaps, which are typical for unmanaged and uneven-aged old-growth forests where large-scale natural disturbances are present, but rare.

(2) Based on the analysis of spatial inhomogeneity, we showed that the influence of the explanatory environmental covariates (longitude, latitude, elevation, northness and eastness) varied between the two reserves due to their different topography and specific site conditions (e.g., talus vs. karst terrain). Moreover, these point pattern analyses revealed that the local densities of the small living trees are influenced by a wider range of environmental covariates (including latitude, elevation and aspect) than those of the small dead trees (i.e., mainly latitude) or the large (dead and living) trees.

(3) With the analysis of neighborhood interactions, we demonstrated significant interactions between small and large trees in both forest reserves. Small living trees showed a random pattern around large dead trees over a broad range of distances and, in one reserve, even dispersion at certain distances. Small living trees further showed clustering around large living trees at short distances and dispersion at large distances. Small dead trees showed predominantly a random pattern, with a tendency to cluster around large living and large dead neighboring trees at short distances. The weakening of clustering with increasing distance indicates that the neighborhood interactions between trees are scale-dependent and reflect different topography as well as the peculiar site conditions of the reserves.

Overall, our study emphasizes the importance of extensive and detailed spatial data on tree regeneration to reveal topographical influences on tree density and detect neighborhood interactions. Such data are not often recorded in forest inventories due to the sheer effort required, although tree regeneration represents a crucial stage of tree life and is ultimately a key factor of forest stand dynamics. With this study, we demonstrated the importance of considering gap size, spatial inhomogeneity and neighborhood interactions when investigating the spatial ecology of mortality in small-sized trees.

CRediT authorship contribution statement

Eva Bianchi: Conceptualization, Methodology, Investigation, Formal analysis, Visualization, Writing - original draft. Harald Bugmann: Funding acquisition, Conceptualization, Writing - review & editing. Martina Lena Hobi: Data curation, Writing - review & editing. Christof Bigler: Funding acquisition, Conceptualization, Methodology, Formal analysis, Supervision, Writing - review & editing.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Data accessibility

The datasets of the forest reserves of Scatle and Bödmerenwald are property of WSL Birmensdorf (Hobi et al., 2020), while the datasets of the environmental variables in swisstopo (Swiss Federal Office of Topography).


