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Tree regeneration potential in urban spruce-dominated forests is shaped by management history

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ABSTRACT

With projected climate change, urban spruce-dominated forests are facing increasing risks of forest damages, encouraging management for mixed stand structures. In the major cities of southern Finland, forests are preferentially maintained continuously covered, and tree regeneration is mostly reliant on naturally emerging sapling stock. To understand the role of forest management in shaping natural tree regeneration in urban forests, we studied the occurrence and abundance of tree saplings in spruce-dominated tree stands on a management continuum ranging from partially logged to undisturbed near-natural stands. Study sites (N = 74) were located in three urban centers in southern Finland: Tampere, Lahti and Helsinki region. We analyzed the data by comparing tree regeneration potential between management classes reflecting the timing and intensity of past logging, and by relating the occurrence of saplings with current structures of the living tree stand.

Compared to undisturbed stands, partially logged sites had increased regeneration of broad-leaved trees and repressed regeneration of spruce, while the most abundant sapling tree species across all management classes was rowan. We conclude that partial logging can be a successful way of directing tree regeneration towards lower dominance of spruce. However, when the canopy is only partially opened, created gaps may end up being filled primarily by rowans that are comparatively shade-tolerant. Because the ingrowth of rowan and many other broad-leaved tree species is strongly restricted by dense populations of large browsing animals in non-urban areas, urban forests may develop stand structures and tree species composition that are otherwise rare in the Fennoscandian boreal forests.

1. Introduction

Urban forests, in the Nordic context, are tree-dominated green spaces characterized by natural or semi-natural forest vegetation (Lehvävirta, 2007). Retained as green areas within and around cities, they alleviate many problems associated with highly built-up landscapes (Tyrväinen et al., 2005). Even though urban forests are often viewed as rather static green backgrounds to built-up areas, they are inherently dynamic systems that are constantly changing as their constituent trees grow, die and regenerate.

Recently, there has been growing concern over the resilience of urban forests in northern Europe due to increasing risks of weather and pest related tree mortality events with projected climate change (Venäläinen et al., 2020). These risks are especially severe for Norway spruce (*Picea abies* (L.) H. Karst.), which is the dominant tree species across a large proportion of forests in the European boreal zone. Increasing the amount of mixed stand structures through active intervention has therefore become an important agenda in forest management, also in urban areas.

Drastic stand-replacing management actions are usually not well received by the public in the larger cities of the Nordic region (Gundersen and Frivold, 2008), and urban forests are preferentially maintained continuously covered. Recruitment of new canopy trees relies primarily on pre-existing, naturally regenerated sapling stock. Tree regeneration can be encouraged by active management actions like thinning or creation of small gaps, but in many places, stands have been left to develop freely with minimal intervention, i.e., removing only hazardous trees one or few at a time. Enabling adequate space for generating new tree generations without losing 'the feel of the forest' due to excessive canopy opening and loss of old dominant trees is one of the main practical challenges of urban forest management.

In this study, we aimed to clarify these trade-offs by studying to how

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tree regeneration potential, i.e., the availability and species composition of naturally occurring tree saplings and juvenile subcanopy trees, depends on management intensity in spruce-dominated forests. To do this, we surveyed saplings and juvenile trees in 74 urban forest sites on a management continuum ranging from near-natural undisturbed sites to sites with varying degrees of partial logging. We then analyzed tree regeneration potential (1) in terms of past management history reflecting the timing and intensity of past logging events, and (2) in terms of present stand structure (basal area and stem density). According to the prevailing rationale of urban forest management, we expected that more intensively logged stands would show higher levels of tree regeneration, especially broad-leaved trees, compared to undisturbed sites due to more open stand structure (Nilson 2001; Eerikäinen et al., 2014).

2. Material and methods

2.1. Study plots

74 study sites were selected from three urban centers in southern Finland (Fig. 1): Tampere (473 residents per km^2), Lahti (261 residents per km^2) and Greater Helsinki (cities of Helsinki, Vantaa and Espoo; 1 581 residents per km^2) (StatFin, 2022). We targeted city-owned forest stands with *Myrtillus* type (MT) or *Oxalis-Myrtillus* type (OMT) vegetation (Cajander, 1926) and mature (≥60 y old) canopy tree layer of Norway spruce as a mono- or co-dominant tree species. Sites belonged to the cities' green areas, and they were situated within inner urban, outer urban or peri-urban zones around the urban centers according to areal classification by Finnish Environment Institute (Helminen et al., 2020). Norway spruce is the naturally dominant late-successional tree species in mesic upland sites in this region. Other tree species (Table 1) are often present as admixed tree species together with spruce.

We avoided stands with continuous canopy openings, that were larger than a few trees wide, and stands where the forest floor was extensively worn due to trampling. We also avoided stands where logging had occurred within the past three years. To ensure adequate site diversity in terms of stand management, we consulted cities' forest management records to find sites where trees had been logged. Managed sites had been treated by thinning or removal of single trees without creating large continuous canopy gaps. Furthermore, we included protected forest sites (ca. ¼ of all sites) without any recent management. The basal area of living trees in the study sites varied between 17.5 and 48.3 m^2/ha (mean 32.7), and the share of spruce was on average 77%.

In each study site, we established a 0.16 ha study plot consisting of four interconnected 20 m × 20 m square cells. Placement of the cells was adjusted to minimize variability of vegetation types and tree stand structure across the plot area. When possible, cells were arranged in a straight row. If the forest stand was too small to fit the cells in a linear formation, cells were arranged in L-, T- or square formation instead.

2.2. Measurement of forest stand characteristics and tree regeneration

Forest stand characteristics were measured following a protocol adapted from Siitonen et al. (2009) between May and July of 2022. In each 0.16 ha study plot, we measured all living trees with at least 5 cm diameter at 1.3 m height (DBH). Similarly, all cut stumps with at least 10 cm in diameter at cut surface were measured. In addition to tree species and diameter, we determined decay class (from 1 to 5) for cut stumps by penetrating a knife into the wood (Renvall, 1995; Table 2).

We measured tree saplings in four 5 m × 5 m square plots placed in the middle of each 20 m × 20 m square cell within the 0.16 ha study plot. We recorded all saplings and juvenile trees that were at least 50 cm tall but less than 5 cm in DBH. We measured DBH for juvenile trees that were 2 m or taller, and height for smaller saplings.

In the 5 m × 5 m plots, we estimated cover percentages of dwarf shrubs, herbaceous vascular plants, forest bryophytes and organic litter, bryophytes indicating paludification (*Sphagnum* spp. and *Polytrichum commune*), and unvegetated bare ground (worn paths, stone surfaces, exposed mineral soil). As a measure of potential edge influence

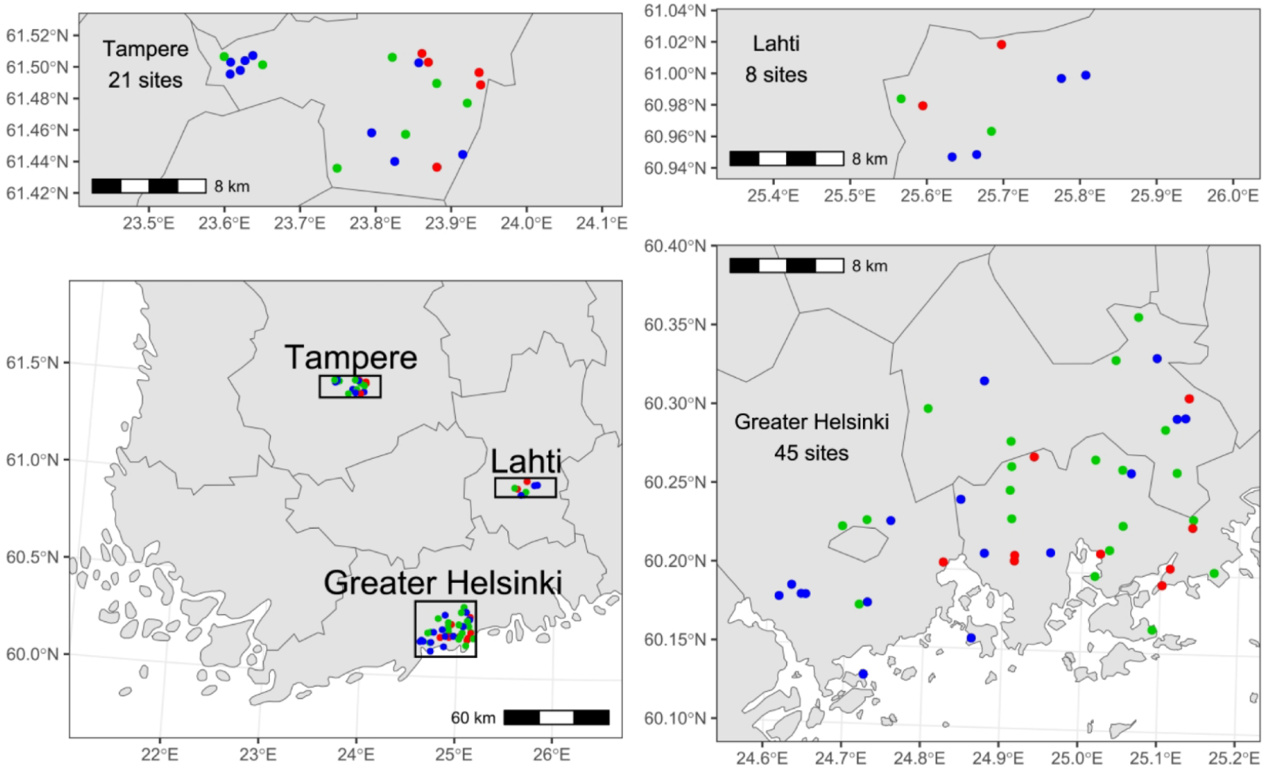

Fig. 1. Locations of the study sites in southern Finland. Red points denote undisturbed forest stands, green points intermediate stands, and blue points managed stands. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

Table 1
Tree species and their traits. Listed species are commonly found in urban spruce dominated stands.

Tree species		Foliage type	Maximum height (m)[a]	Shade tolerance (0–5 scale)[b]	Seed dispersal mode	Root suckering ability
Norway spruce	*Picea abies* (L.) H. Karst.	Needle	> 25	4.45	Wind – medium winged seed	No
Scots pine	*Pinus sylvestris* L.	Needle	> 25	1.67	Wind – medium winged seed	No
Silver birch	*Betula pendula* Roth	Broad	> 20	2.03	Wind – small winged seed	No
Downy birch	*Betula pubescens* Ehrh.	Broad	> 20	1.85	Wind – small winged seed	No
Eurasian aspen	*Populus tremula* L.	Broad	> 20	2.22	Wind – minute fluffed seed	Yes
Pedunculate oak[c]	*Quercus robur* L.	Broad	> 20	2.45	Rodent and bird vectored	No
Norway maple[c]	*Acer platanoides* L.	Broad	> 20	4.2	Wind – large winged seed	No
Rowan	*Sorbus aucuparia* L.	Broad	< 15	2.73	Bird vectored	Yes
Goat willow	*Salix caprea* L.	Broad	< 15	2.16	Wind – minute fluffed seed	No

[a] values considered typical in the study area (southern Finland).
[b] values from Niinemets and Valladares (2006).
[c] relatively rare as forest trees, primarily associated with fertile soils, southerly species in Finland.

Table 2
Definitions of wood decay classes, adapted from Renvall (1995).

Decay class	Definition
1	hard, a knife penetrates by pushing only a few mm into the wood
2	relatively hard, knife penetrates 1–2 cm
3	relatively soft, knife penetrates 3–5 cm
4	soft throughout
5	very soft, can be moulded by hand

(Lehvävirta et al., 2014) on a study plot, we measured the proportion of forested area within 50 m radius from the midpoint of each 0.16 ha study plot. Calculation was based on Corine land cover data (Copernicus Land Monitoring Service, 2018). Lower proportion of forested area was assumed to indicate higher proportion of open land around the study area, and hence, stronger edge influence.

2.3. Site management classes

Forest sites were assigned to three management classes based on the amounts and decay class distribution of cut tree stumps, which reflect the intensity and timing of past logging activity (Bader et al., 1995). Stands that had no cut stumps in decay classes 1–3 were classified as undisturbed (no recent management). Stands with at least 1 m^2/ha basal area of cut stumps in decay classes 1 or 2 were classified as managed (recent, relatively intensive logging). Rest of the sites were classified into an intermediate class, where recent logging had been relatively mild and the signs of more intensive logging were older (stumps mostly in decay class 3 or further).

2.4. Statistical analyses

All analyses were done in R (v.4.2.2; R Core Team, 2020). Differences between management classes, in terms of management intensity and timing, and tree stand composition, were illustrated with principal component analysis (PCAs) with R package vegan (v.2.6–4; Oksanen et al., 2022). We used basal areas of cut stumps in different decay classes as variables describing management intensity and timing, and basal areas of different tree species in the living stand as variables describing stand composition. Basal areas (m^2/ha) were square root transformed, centered, and scaled to equal variance before PCA.

Tree regeneration potential in management classes was analyzed individually for tree species by generalized linear mixed models (GLMMs) using R package lme4 (v.1.1–31; Bates et al., 2015). When feasible, we estimated separate models for two different size classes of same tree species, as we presumed that responses of the trees could change from one developmental stage to another. The smaller size class included saplings that were less than 2 m tall. We preferentially focused on larger saplings ($\geq$1 m high) to increase within-group cohesiveness, but allowed a lower minimum height threshold of 0.5 m for tree species that were otherwise too infrequent to be analyzed. The larger size category included small trees that were at least 2 m tall but had DBH less than 5 cm. For the most common tree species, spruce and rowan, we estimated GLMMs for saplings ($1 \text{ m} \leq \text{height} < 2 \text{ m}$) and juvenile trees ($\text{height} \geq 2 \text{ m}$, $\text{DBH} < 5 \text{ cm}$). For Eurasian aspen and silver birch, we estimated GLMMs for saplings ($1 \text{ m} \leq \text{height} < 2 \text{ m}$) only. For infrequent tree species, downy birch, goat willow, Scots pine, pedunculate oak and Norway maple, we estimated GLMMs for saplings with a lowered minimum height threshold ($0.5 \text{ m} \leq \text{height} < 2 \text{ m}$). We used the number of stems as the response variable in GLMMs for rowan, assuming Poisson distribution (with log-link). GLMMs for all other tree species, which were less frequent than rowan, were logistic models with presence–absence as the response variable. Sample unit in all models was the 5 m × 5 m sample plot ($N = 296$).

To test the effect of forest management, we included site management class as an explanatory variable with ‘undisturbed’ as the baseline level (a factor with tree levels: undisturbed, intermediate, and managed). Sample site ($N = 74$) was included as a random factor accounting for non-independence among sample plots within the same site. To account for the effects of other environmental variability, we used a stepwise model construction procedure to further explore which other explanatory variables should be included in the models. Candidate variables were

1. Log_e-transformed stem density (trees with $\text{DBH} \geq 5$ cm) in the 20 m × 20 m plot
2. Proportion of broad-leaved trees in the 20 m × 20 m plot (% of basal area)
3. Site fertility, ascending from MT to OMT to herb-rich vegetation type (numeric; 0–2)
4. Paludification (cover-% of bog mosses inside the 5 m × 5 m plot)
5. Bare ground (cover-% inside the 5 m × 5 m plot)
6. Surrounding forest area, i.e., the proportion of forested land within 50 m radius from the center of the 0.16 ha plot

In addition, we used basal areas (m^2/ha) of aspen and rowan trees in the surrounding 20 m × 20 m cell as candidate variables for aspen and rowan models. This was to account for variability related to the vegetative regeneration strategy of these species, i.e., their habit of forming saplings by suckering from the roots of existing trees.

We used the buildmer() function in R package buildmer (v.2.7; Voeten, 2022) to first identify the maximally informative model capable of converging, and then, to reduce model complexity by stepwise elimination of variables. Variables were tested for elimination based on likelihood ratio tests. Coefficients of determination were calculated for GLMMs with the function rsquared() in R package piecewiseSEM (v.2.1.2; Lefcheck, 2016).

To analyze tree regeneration in terms of the living stand structure (basal area and stem density), and to identify tree-specific optima for regeneration, we estimated generalized additive mixed models

(GAMMs) with R package mgcv (v.1.8-41; Wood, 2011). We estimated GAMMs only for the common tree species, i.e., juvenile trees and saplings of spruce and rowan, and saplings of aspen and silver birch. All GAMMs were estimated as logistic models using presence–absence of saplings or juvenile trees in a study plot as the response variable. We used a tensor product smooth term (Wood, 2006) to capture the effects of stand basal area and stem density jointly. Basal area (living trees with DBH $\geq$ 5 cm; m^2/ha) and stem density (number of stems per ha, $\log_e$-transformed) were calculated individually for each 20 m × 20 m square cell enclosing the 5 m × 5 m sample plots. Management class was not included as an explanatory variable, but a random factor (site) and other variables (see GLMMs) were included if they were included in the respective GLMM.

3. Results

3.1. Characteristics of forest management classes

Classification of forest sites into management classes reflected a gradient of logging intensity, but differences were not as consistent in terms of living stand composition (Fig. 2 A–C). Management classes had significant differences in the basal area of spruce (Kruskal-Wallis chi-squared = 7.3846, df = 2, p = 0.025), which was largest in undisturbed stands, and in the basal area of other trees than spruce (Kruskal-Wallis chi-squared = 11.835, df = 2, p = 0.003), which was largest in intermediate stands (Fig. 2 D). Stem density and quadratic mean diameter of trees were not significantly different, but they tended to increase from managed to intermediate and undisturbed forests (Fig. 2 E).

3.2. Differences in tree regeneration between management classes

Total abundances of saplings ($0.5 \leq$ height < 2 m) and juvenile trees (height ≥ 2 m, DBH < 5 cm) were lowest in undisturbed forests (ca. 4 500 per ha), and roughly twice as high in intermediate (ca. 8 500 per ha) and managed forests (ca. 9 100 per ha). The most abundant and common regenerating tree species across all management classes was rowan, representing over half of all saplings and juvenile trees (Fig. 3).

Based on GLMMs (Table 3, Fig. 4, see Supplementary Material for full model outputs), the effects of stand management on tree regeneration potential were positive for rowan, aspen, and silver birch, but mostly insignificant or negative for spruce. Juvenile spruce trees were suppressed in managed forests, but the occurrence of saplings was not significantly related to management class. Juvenile rowan trees were most abundant in the intermediate management class. Models for infrequent tree species had no significant effects related to forest management, and their explanatory power was generally low.

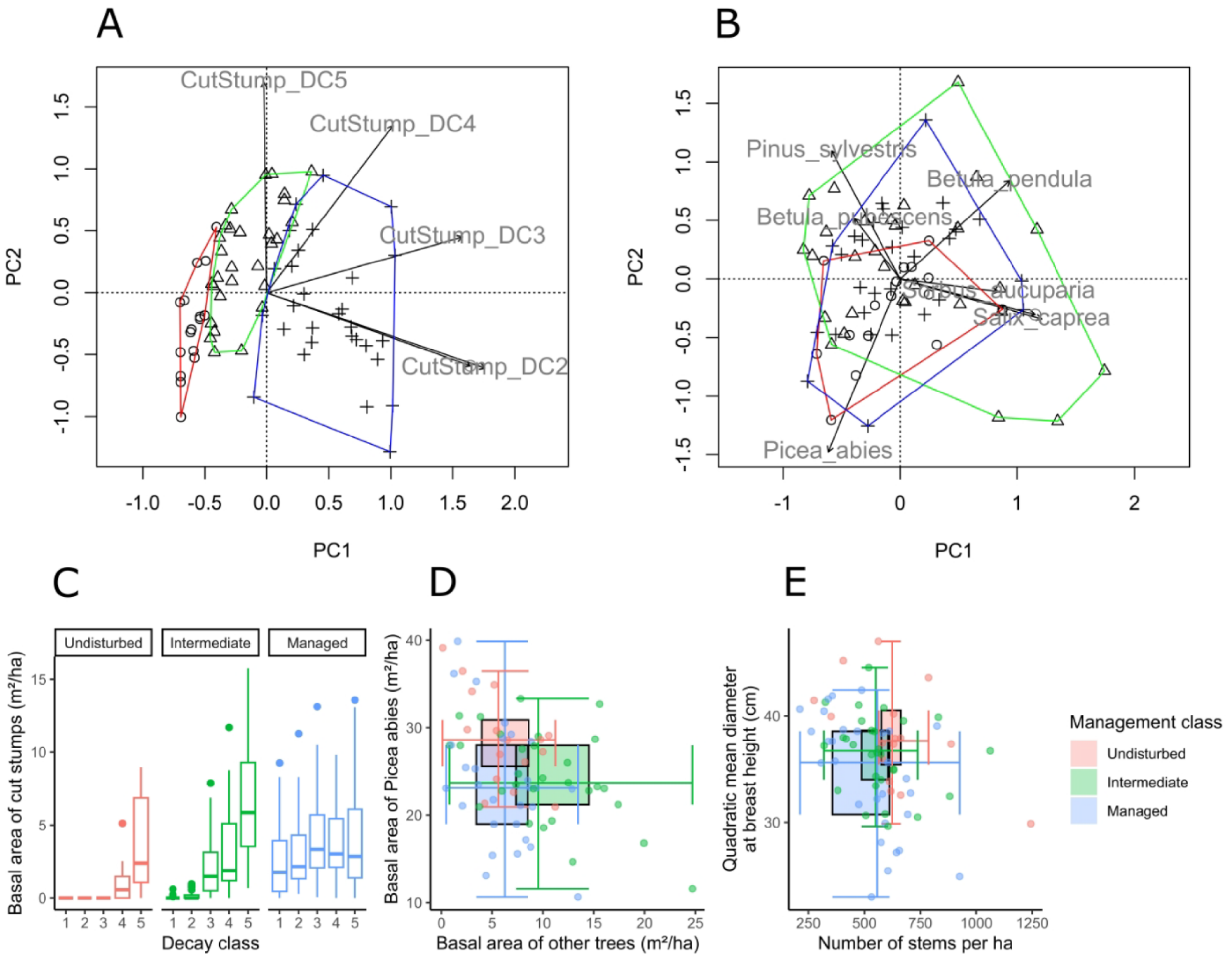

Fig. 2. Forest stand characteristics in three management classes: Undisturbed ($N_{sites} = 16$), intermediate ($N_{sites} = 29$) and managed ($N_{sites} = 29$). Ordination plots (A–B) depict differences between management classes in terms of (A) logging intensity (basal areas of cut stumps in different decay classes) and in terms of (B) living tree composition (basal areas of tree species). In the ordination plots, circles are undisturbed sites, triangles are intermediate sites, and crosses are managed sites. Ranges of variability in stand characteristics are shown quantitatively in boxplots C–E.

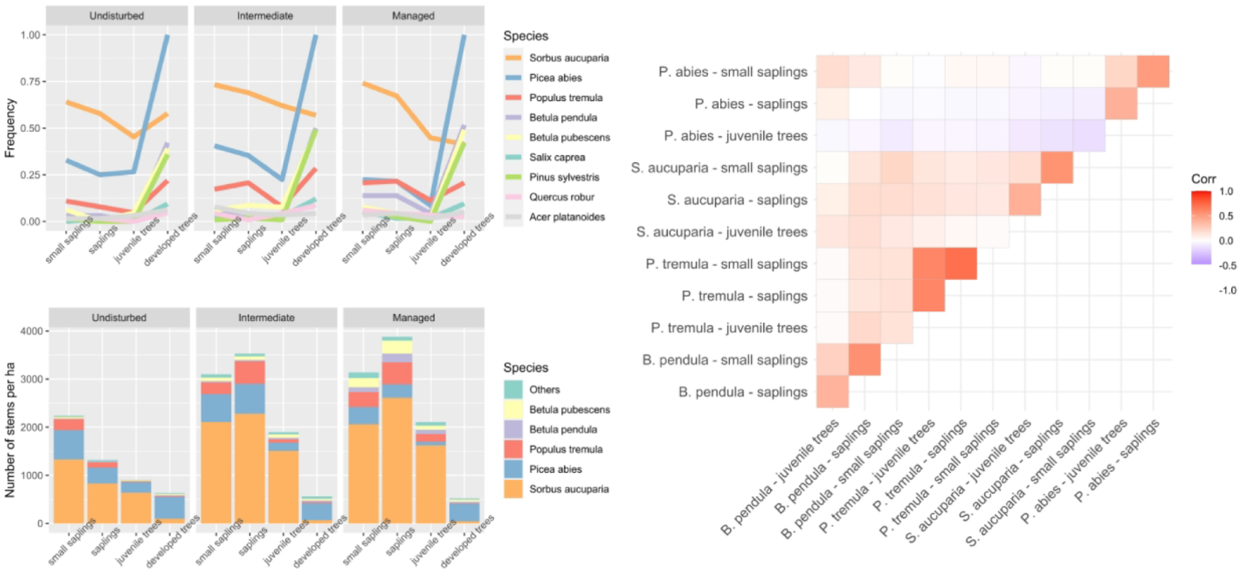

Fig. 3. Frequencies and abundances of small saplings (0.5 ≤ height < 1 m), saplings (1.0 ≤ height < 2 m), juvenile trees (height ≥ 2 m, DBH < 5 cm) and developed trees (DBH ≥ 5 cm) in forests across management classes, and correlations of saplings co-occurrence in sample plots. Frequency describes the proportion of plots where stems were present, and abundance describes the density of stems averaged over the summed inventory area. Co-occurrence patterns among saplings of the four most frequent tree species are depicted in the correlation (Kendall's T) plot.

Table 3
Effects of forest management class and stem density on saplings and juvenile trees based on GLMMs. Model type and coefficients of determination are shown in columns 2–4. Marginal R^2 represents the proportion of variance explained by fixed effects alone, and conditional R^2 represents the proportion of variance explained by fixed and random effects (site) together. Model coefficients (columns 5–8; coeff. ± SE) are shown in bold when $p < 0.05$ and underlined when $0.05 \leq p < 0.10$. Coefficients of management class describe how intermediate and managed forests differ from undisturbed forests. See text for other model coefficients.

				Model coefficients			
Tree species	Model type	Marg. R^2	Cond. R^2	Intercept	Management class Intermediate	Management class Managed	$\log_e$(Stem density)
Common tree species							
Norway spruce (*Picea abies*)							
saplings (1 m ≤ height < 2 m)	logistic	0.02	0.31	**−1.48 ± 0.51**	0.63 ± 0.62	−0.32 ± 0.63	
juvenile trees (height ≤ 2 m, DBH < 5 cm)	logistic	0.10	0.22	**−10.53 ± 3.49**	−0.16 ± 0.53	**−1.41 ± 0.61**	**1.45 ± 0.53**
Rowan (*Sorbus aucuparia*)							
saplings (1 m ≤ height < 2 m)	Poisson	0.18	0.89	**6.42 ± 0.78**	**0.88 ± 0.40**	**0.91 ± 0.40**	**−1.00 ± 0.11**
juvenile trees (height ≤ 2 m, DBH < 5 cm)	Poisson	0.11	0.89	**3.87 ± 0.91**	**1.17 ± 0.50**	0.59 ± 0.51	**−0.70 ± 0.13**
Eurasian aspen (*Populus tremula*)							
saplings (1 m ≤ height < 2 m)	logistic	0.14	0.28	**−3.32 ± 0.68**	1.02 ± 0.70	1.33 ± 0.70	
Silver birch (*Betula pendula*)							
saplings (1 m ≤ height < 2 m)	logistic	0.06	0.06	6.61 ± 3.50	0.34 ± 0.86	1.40 ± 0.78	**−1.62 ± 0.57**
Infrequent tree species saplings (0.5 m ≤ height < 2 m)							
Downy birch (*Betula pubescens*)	logistic	0.02	0.39	10.72 ± 7.51	0.51 ± 1.80	−0.16 ± 1.87	**−2.88 ± 1.26**
Goat willow (*Salix caprea*)	logistic	<0.01	0.05	**−8.21 ± 2.55**	0.21 ± 2.48	1.24 ± 2.29	
Scots pine (*Pinus sylvestris*)	logistic	<0.01	0.05	**−8.36 ± 2.58**	0.52 ± 2.47	1.02 ± 2.38	
Pedunculate oak (*Quercus robur*)	logistic	0.07	0.59	**−6.85 ± 2.22**	1.90 ± 1.80	1.91 ± 1.81	
Norway maple (*Acer platanoides*)	logistic	0.05	0.27	**−5.21 ± 1.16**	1.58 ± 1.08	1.25 ± 1.11	

3.3. Effects of other site characteristics

In addition to management class, stem density (trees with DBH ≥ 5 cm) in the 20 m × 20 m cell emerged as a significant predictor for spruce (juvenile trees), rowan, silver birch and downy birch (Table 3). Large stem density had a positive effect on spruce and negative effects on other species (Fig. 5). Paludification decreased the abundance of rowan saplings (Coeff. ± SE = -16.11 ± 2.64, $p < 0.001$) and juvenile rowan trees (Coeff. ± SE = -14.67 ± 3.80, $p < 0.001$), but increased the occurrence probability of aspen (Coeff. ± SE = 41.06 ± 22.59, $p = 0.07$) and oak (Coeff. ± SE = 34.59 ± 16.22, $p = 0.03$) saplings. Higher site fertility increased the occurrence probability for maple saplings (Coeff. ± SE = 1.14 ± 0.51, $p = 0.02$). Larger proportion of bare ground in study plots decreased the abundance of rowan (Coeff. ± SE = -0.70 ± 0.33, $p = 0.04$) and the probability of occurrence of oak saplings (Coeff. ± SE = -9.20 ± 5.34, $p = 0.08$). Basal area of larger (DBH ≥ 5 cm) conspecific trees in the 20 m × 20 m plot was a significant positive predictor for aspen saplings (Coeff. ± SE = 0.28 ± 0.08, $p < 0.001$) and juvenile rowan trees (Coeff. ± SE = 0.12 ± 0.04, $p < 0.001$), but not for rowan saplings. Proportion of broad-leaved trees or proportion of forested land around the study plots (within 50 m radius) were not significant predictors for any tree species. A large proportion of the explanatory power in most models was related to random effects (Table 3) indicating that tree regeneration was strongly affected by stand-scale processes that could not be captured by any of the measured environmental variables.

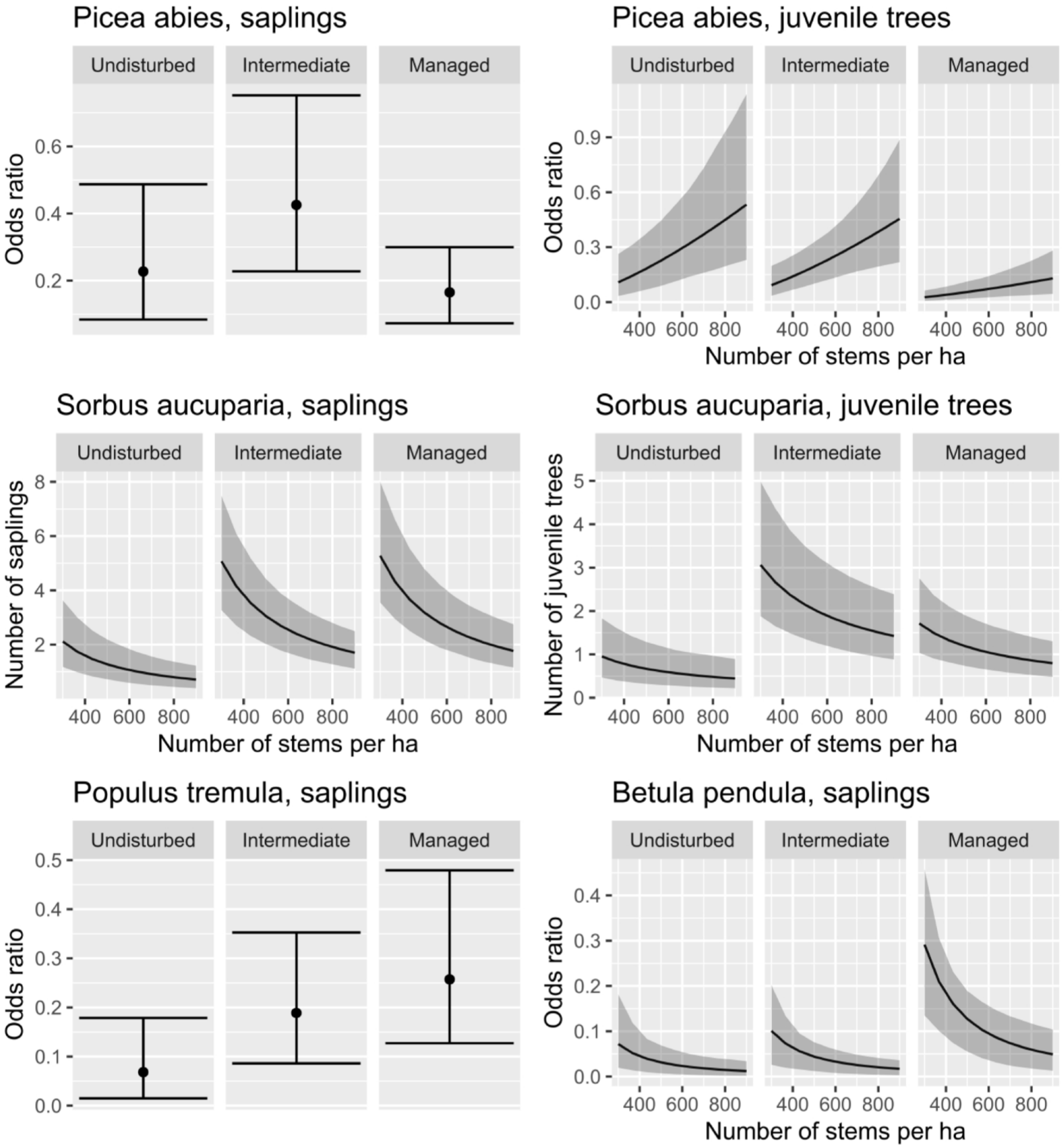

Fig. 4. Model predictions for saplings (1 m ≤ height < 2 m) and juvenile trees (height ≤ 2 m, DBH < 5 cm) based on GLMMs. Predictions show the expected number (for rowan) or odds ratio of presence–absence (for other species) for stems in a 5 m × 5 m sample plot. Assumptions in all predictions are that site vegetation type is MT, and that sample plot has no worn or paludified ground cover. The effect of forest stem density (trees with DBH ≥ 5 cm) in the surrounding 20 m × 20 m cell is illustrated in the plot when it was included in the model (see Table 3). Error bars and bands show 90% prediction interval based on 1000 bootstrap replications.

3.4. *Tree regeneration potential in relation to forest basal area and stem density*

Optimal stand structures for tree regeneration differed among tree species (Fig. 5). Spruce was, in general, positively associated with large stem density, but the strength of this association was dependent on stand basal area. Stands with large basal area were optimal for spruce saplings, whereas juvenile spruce trees preferred small basal area. Of all the analyzed species, silver birch was most clearly associated with open stand structure, i.e., stands with the smallest basal area and stem density. Rowan saplings preferred small stem density and large stand basal area, whereas juvenile rowan trees showed little response to stem density but preferred small basal area. Responses of aspen were complex with a higher optimum in the most densely packed stand structure, i.e., with the largest basal area and stem density, and a lower optimum in the most open stand structure. Model results and diagnostics are provided in Supplementary Material.

4. Discussion

4.1. *Regeneration potentials of tree species in urban spruce stands*

Tree regeneration potential in urban spruce-dominated forests changed markedly along a gradient from undisturbed to recently logged stands, with an overall increase in sapling abundances and an associated shift in species composition. Average numbers of tree saplings in all

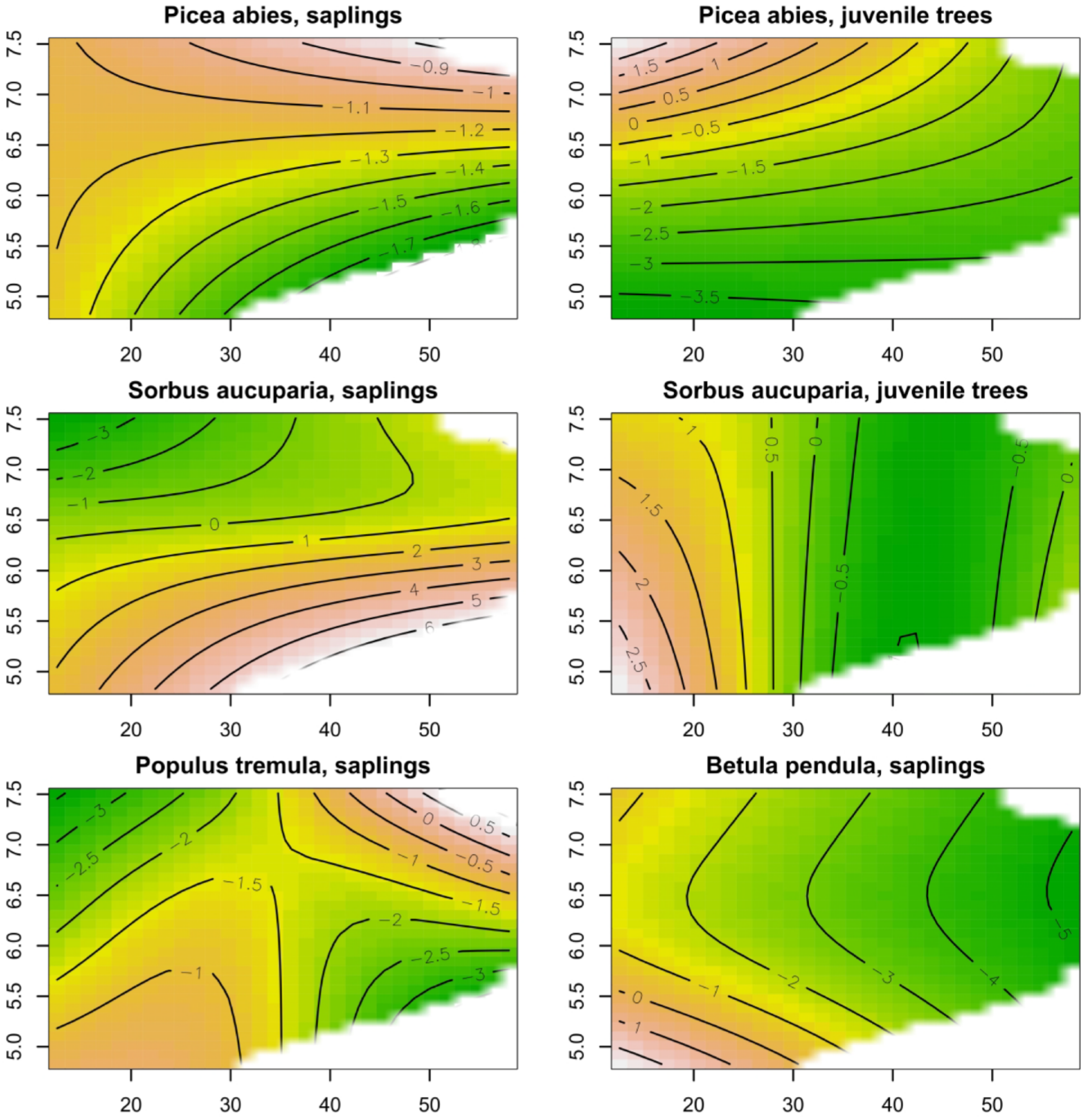

Fig. 5. Heatmaps of predicted log-odds and abundances for saplings (1 m ≤ height < 2 m) and juvenile trees (height ≤ 2 m, DBH < 5 cm) across gradients of stand basal area (x-axis; m^2/ha) and stem density (y-axis; $\log_e$(number of stems per ha)) based on GAMMs. Predictions describe the probability of occurrence of saplings or juvenile trees in 5 m × 5 m sample plots. Orange color indicates higher and green color lower predicted values. Assumptions in all predictions are that site vegetation type is MT, and that sample plot has no worn or paludified ground cover. For rowan and aspen, basal area of respective tree species (trees with DBH ≥ 5 cm) in the surrounding 20 m × 20 m cell was set to the median value of those sites where their basal area was > 0. Predictions have been plotted with site-specific random effects removed. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

three management categories were somewhat higher than those reported from rural uneven-aged spruce stands by Lähde et al. (2002), ca. 1 300 per ha (height ≥ 1.3 m, DBH < 9 cm). Respective numbers of saplings, in the same size range, were 1 800, 3 700 and 4 400 saplings per ha in undisturbed, intermediate, and managed urban stands. However, only a minority of the saplings in urban forests were spruce (600, 500 and 250 saplings per ha) or other tall canopy-forming tree species, such as aspen, birches or pine.

Regeneration of broad-leaved trees was generally strongest in the most intensively logged stands (managed sites), whereas regeneration potential of spruce was greatest in forests that were undisturbed or only mildly logged (intermediate sites). Contrasting results regarding spruce and broad-leaved tree regeneration can be related to differences in their ecology, but this pattern could also be influenced by deliberate management.

In managed urban stands, forests undergrowth may be purposefully cleared out to improve visibility within the forest (see Tyrväinen et al., 2003; Koivula et al., 2019). The effects of undergrowth removal may be relatively long-lasting for spruce, as conifers tend to recover and grow more slowly than broad-leaved trees. Although we avoided stands that had evident signs of recent undergrowth removal, we cannot rule out the possibility that our results could be influenced by older clearing operations.

Both spruce and broad-leaved tree species are expected to benefit from canopy opening (Löf et al., 2007; Pukkala et al., 2013; Eerikäinen et al., 2014), but faster growth rates of broad-leaved tree saplings allow them to respond to increased light availability more quickly than spruce (see Pacala et al., 1994). In earlier studies, dense thickets of broad-leaved tree saplings have been proposed as a potential hindrance for spruce regeneration in urban forests (e.g., Lehvävirta et al., 2004; Hauru et al., 2012; Hamberg et al., 2015). However, co-occurrence patterns of saplings in our data do not support this view. Instead, there seemed to be a stronger restricting effect exerted by taller spruce saplings on smaller broad-leaved saplings than the other way round (Fig. 3).

Broad-leaved tree species generally responded positively to stand management, but the strength of the association varied among species. Managed and open-structured stands were most clearly favored by silver birch, consistent with its poor shade-tolerance (Hynynen et al., 2010). Aspen and rowan were also more common in managed and intermediate sites than in undisturbed sites, but their responses were generally less pronounced, and more complex with regard to stand structure.

Consistent with earlier studies (e.g., Hamberg et al., 2015), rowan saplings tended to occur most commonly in stands with large basal area, possibly because seed-dispersing birds prefer them as roosting sites and because competing vegetation in the field-layer is often sparse (Żywiec and Ledwoń, 2008). However, further development of rowan into juvenile trees was evidently favored by less dense stand structure.

Significant positive association between the presence of aspen saplings and larger aspen trees suggests that most of the observed aspen saplings may have been vegetatively regenerated root suckers. Spatial patterns in the emergence of aspen saplings may thus be more strongly determined by the availability of mother trees than by forest structure per se (Qinghong and Hytteborn, 1991; Lehvävirta et al., 2004). In contrast, lack of association between rowan saplings and larger conspecific trees probably reflects prolific initial establishment through seeds in this tree species. However, positive association with juvenile rowan trees and larger rowan trees suggests that vegetatively produced saplings may have higher survival rates or faster growth rates compared to seed-borne saplings.

Beyond management history or stand structure, tree regeneration potential was also affected by local site conditions such as paludification, which can introduce intrinsic heterogeneity in tree species composition both within and between stands. Furthermore, more variation was generally explained by stand-level random effects than by measured environmental variability. This stresses the importance of random processes or other unmeasured variability in shaping tree regeneration at the stand scale. Such processes could include, for instance, spatial and temporal variation in seed availability.

4.2. Management implications

Forest sites included in this study are probably representative of management levels currently prevailing in the urban spruce-dominated forests of the largest cities of southern Finland. Wood production has been relatively insignificant management target for these forests already for decades, as higher priorities have been given to recreational and biodiversity values (Gundersen et al., 2005). Low levels of wood harvesting have allowed urban tree stands to age relatively freely, and consequently, mature spruce-dominated stands are now probably the most common forest type in urban areas across much of the boreal Nordic region.

Regarding tree regeneration potential, our results suggest that in the absence of major disturbances, the reservoir of sapling becomes increasingly dominated by rowan and spruce. With only minor disturbances, i.e., removal or death of single trees at a time, spruce is expected to retain or increase its dominance in the upper canopy (Kuuluvainen, 1994; Kuuluvainen and Aakala, 2011). However, when adequate spruce undergrowth is lacking, retaining the forest continuously covered may lead to a situation where the gradual thinning of spruce canopy is compensated mostly by rowans.

Rowans require relatively small openings to reach maturity (Holeksa et al., 2017) and likely benefit from dynamics where newly formed canopy gaps are initially small and expand incrementally (Żywiec and Ledwoń, 2008). Partial replacement of old spruce-dominated canopies with much shorter rowan trees could increase stand structural heterogeneity and also result in significant changes in the visual quality of the forest landscape. Overall, forests with high proportion of rowan are rather rare in Fennoscandia, and they are usually associated with spontaneous ruderal afforestation. Furthermore, in non-urban areas, the growth of rowans is often restricted by heavy browsing pressure from moose (*Alces alces*) (Linder et al., 1997; Heikkilä et al., 2003; Angelstam et al., 2017). From this point of view, the potential success of rowan as a (mixed) canopy tree in formerly spruce-dominated urban stands could contribute positively to forest habitat diversity at regional scales (see Götmark et al., 2005; Angelstam et al., 2017). However, smaller browsing ungulates such as roe deer (*Capreolus capreolus*) are better adapted to urbanized landscapes (Tinoco Torres et al., 2011) and can reach high densities in urban and peri-urban areas, where predation and hunting pressure is relaxed (Carpio et al., 2021).

The emergence of more diverse broad-leaved undergrowth can be stimulated by disturbances such as partial logging. However, the ingrowth of more light-demanding trees into the forest canopy can require compromises between maintaining the forest continuously covered and providing adequate space for the shade-intolerant trees. In practice, ingrowth of shade-intolerant tree species, such as Scots pine and most broad-leaved trees, may necessitate relatively frequent removal of competing trees, or alternatively, creation of canopy gaps that are initially quite large (Eerikäinen et al., 2014). For instance, simulations by Rämö and Tahvonen (2015) suggest that keeping the basal area of spruce at 20 m^2/ha or less would allow broad-leaved tree species to gradually gain dominance. In this study, such conditions were met in some of the least spruce-dominated stands in managed and intermediate management classes.

5. Conclusions

In this work, we have showcased how forest management shapes natural sapling pools in the understoreys of urban spruce-dominated stands. According to our expectations, regeneration of broad-leaved trees was more prolific in partially logged than in undisturbed stands. However, this effect seemed to be relatively transient for light-demanding tree species, such as silver birch and aspen, but more durable for rowan, which seems to be well adapted to low-intensity disturbances. We suspect that repressed regeneration potential of spruce especially in the most intensively managed sites may be the result of active clearing or accidental destruction of saplings during logging operations.

CRediT authorship contribution statement

Aku Korhonen: Conceptualization, Methodology, Investigation, Formal analysis, Writing – original draft, Funding acquisition. **Heli Vuorilampi:** Investigation. **Oskar Katavisto:** Investigation. **Auli Immonen:** Data curation, Formal analysis, Writing – review & editing. **Leena Hamberg:** Conceptualization, Supervision, Funding acquisition, 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.

Data availability

Data will be made available on request.

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Appendix A. Supplementary data

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