Contents lists available at ScienceDirect

Biological Conservation

journal homepage: www.elsevier.com/locate/biocon

Tree and stand characteristics jointly predict tree-related microhabitats on retention trees in production forests

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ARTICLE INFO

ABSTRACT

Retention forestry emerged as a means of ameliorating the biodiversity impacts of clearcutting 30 years ago and has become an integrated part of forest management in many countries. Nowadays, there is still an increasing need to assess to what extent retention trees contribute to biodiversity in production forests. We used tree-related microhabitats (TreMs), as an indicator of the potential of the forest to host taxonomic biodiversity, to better understand the effect of broadleaf retention trees, and surrounding conditions derived from stand management, on biodiversity. We inventoried TreM types on 114 retention trees of four broadleaf tree taxa (*Betula* spp., *Fagus sylvatica*, *Quercus* spp., and *Populus tremula*) located within 20 even-aged conifer-dominated production forests (*Picea abies*) in southern Sweden. We evaluated the effect of retention tree attributes (species and age) and of the surrounding environment (production tree density and distance to the retained trees) on the diversity of TreM types and groups. We found that retention tree species with different characteristics and physiological niche (light-demanding vs. shade-tolerant and pioneer vs. late-successional) developed distinct TreM assemblages. TreM diversity increased significantly with increasing retention tree age and surrounding tree density. Higher surrounding tree density is particularly related to some TreMs either positively (crown deadwood, bryophytes) or negatively (buttress-root concavities, lichens). Overall, the extent that retention forestry potentially contributes to forest biodiversity will depend on promoting different broadleaved retention tree species and managing surrounding trees accordingly to allow retention trees to become older and maintain TreMs in the long term.

1. Introduction

Production forests are socio-ecological systems that provide essential ecosystem services such as woody biomass, climate regulation, and environments for recreation (Brockerhoff et al., 2017). In intensively managed production forests, provisioning services are often prioritized at the expense of biodiversity and other ecosystem services (Felton et al., 2024). In the process, silvicultural practices tend to simplify forest structures and remove elements characteristic of old-growth forests, potentially limiting the capacity of such forests to provide habitat for biodiversity (Brockerhoff et al., 2017; Deal et al., 2013; Gustafsson et al., 2010). Since we currently face a global crisis of biodiversity loss and

production forest cover continues to increase worldwide, there is a broad consensus on the need to safeguard and promote biodiversity in these management systems (FAO, 2020; Muys et al., 2022).

In Fennoscandia, production forests mostly consist of stands of even-aged conifer-dominated monocultures that are mechanically clear-cut (Gustafsson and Perhans, 2010; Simonsson et al., 2015). To mitigate the negative effects of clearcutting on biodiversity and incorporate conservation measures into production forests, retention forestry is widely applied in this context (Gustafsson and Perhans, 2010; Vanha-Majamaa and Jalonen, 2001). First proposed in North America (Franklin, 1989), retention forestry promotes structural diversity and habitat for biodiversity ("life-boating" effect), as well as ecosystem

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functioning and landscape connectivity by retaining single or groups of trees at the time of harvest, often as living trees (green tree retention, GTR) (Gustafsson et al., 2012; Vanha-Majamaa and Jalonen, 2001), although no specific regulations protect retention trees for more than one rotation (Beese et al., 2019). Despite the importance of old trees for forest biodiversity (Bütler et al., 2013; Lindenmayer and Laurance, 2017; Lindenmayer et al., 2014) and the retention approach as a means of increasing their presence in production forests (Fedrowitz et al., 2014), there are still many remaining questions about the potential contribution of retention trees to biodiversity in the longer term.

A large number of studies have assessed the effects of retention forestry on biodiversity (Fedrowitz et al., 2014). However, conventional studies are usually limited to particular taxa, such as mammals, birds, or vascular plants, whereas other taxonomic groups, including reptiles and fungi, are underrepresented (Fedrowitz et al., 2014; Gustafsson et al., 2020a, 2020b). In response, tree-related microhabitats (TreMs) have been proposed as an indicator of the potential of the forest to host taxonomic biodiversity (Asbeck et al., 2021). TreMs are structures that occur either on living or standing dead trees and constitute an essential habitat for numerous species at some point in their life cycle (Larrieu et al., 2018). Injuries, crown deadwood, excrescences, or epiphytic structures are just a few of the seven general forms of TreMs that have been documented to host insects, arachnids, birds, mammals, amphibians, fungi, nematodes or reptiles (Bütler et al., 2020; Larrieu et al., 2018; Majdi et al., 2024). The underlying concept of microhabitats born by trees is not new, and there is extensive research on the relationship of some taxa with some TreMs, for example tree cavities (Wesołowski, 2007) and dendrotelms (Kitching, 1971). However, the novelty of the TreM concept resides in (i) considering TreMs as key habitat resources at the forest stand level, interacting with other habitat resources such as deadwood items (Larrieu, 2014), and (ii) the hierarchical typology that Larrieu et al. (2018) developed – 47 TreM types organized in 15 groups and seven general forms – which has contributed to its standardization and ready applicability to answering questions involving forest biodiversity.

TreMs are old-growth attributes essential to fostering habitat heterogeneity and biodiversity in production forests, while also playing an important role in ecosystem functioning (Asbeck et al., 2021; Larrieu et al., 2018). Despite their importance, forest management is not always targeted towards promoting TreMs. Conventional forest management strategies can limit TreM development by removing trees of low economic value, as well as those trees that compete for resources with production stems, or senescent trees that may pose safety risks to forest personnel (Cosyns et al., 2020). In contrast, new management strategies with higher conservation ambition can actively promote TreM-bearing trees spanning different tree species, sizes and ages (Asbeck et al., 2021). There is thus a close relationship between forest management decisions and conservation goals and the resultant density and diversity of TreMs (Cosyns et al., 2020; Courbaud et al., 2022; Larrieu and Cabanettes, 2012). In this context, there is an urgent need to better understand the factors influencing TreM occurrence in production forests, to provide forest managers and policymakers with practical recommendations for the conservation of TreM-associated biodiversity.

Several studies have used the TreM approach to assess biodiversity in production forests, particularly in the temperate forests of central Europe (France, Germany and Italy; Larrieu et al., 2012; Paillet et al., 2018; Regnery et al., 2013; Winter and Möller, 2008). However, a major research gap persists in boreal and hemiboreal forests where few TreM related studies have been conducted (see Martin et al. (2021); Michel and Winter (2009) in North America and Kõrkjas et al. (2021); Kõrkjas et al. (2023); Lilja and Kuuluvainen (2005) in Europe). For example, the contribution of retention trees to the occurrence of TreMs has not been studied in even-aged production forests located in a hemiboreal context.

In this study, we quantified and categorized TreM occurrence on retention trees located within even-aged Norway spruce (*Picea abies*) dominated production stands to better understand the habitat

contribution of retention trees, as well as the influence of proximate stand management, on habitat provision for biodiversity. Specifically, we 1) evaluated the effect of attributes of retention trees, including tree species and age, on the provision of TreMs, and 2) assessed the effects of the surrounding environment derived from forest management (e.g., production tree stem density and distance to the retained trees) on the diversity of TreMs borne by retention trees. Ultimately our aim was to provide practical recommendations regarding how to enhance biodiversity in production forests.

2. Methodology

2.1. Study area

The study was performed in 20 production stands dominated by Norway spruce in southern Sweden (Fig. 1). The stands are located in the hemiboreal zone, a transition zone between the boreal and temperate biomes (Ahti et al., 1968). Mean temperatures range from -1 °C in winter to 17 °C in summer whereas mean annual precipitation vary between 600 mm in the southern and eastern stands, to 800 mm in the western stands (SMHI, 2019). The stands were harvested 23–34 years ago leaving broadleaf retention trees at a density of approximately 10 trees per hectare, and then planted with Norway spruce. The height of the spruce trees ranged between 10.8 and 19.4 m (16.7 ± 3.0 m on average). Since the previous final timber harvest and subsequent planting, no other management interventions have occurred (i.e., no thinning of competing vegetation was conducted before this study). For this study, we focused on the most common broadleaf tree taxa that are selected as retention trees in production stands in this region (Gustafsson et al., 2020b): aspen (*Populus tremula*), European beech (*Fagus sylvatica*), birch (*Betula pendula* and *B. pubescens*), and oak (*Quercus robur* and *Q. petraea*). In addition, we selected retention trees that were (i) of >25 cm diameter at breast height (DBH), (ii) solitary and (iii) surrounded by production conifer trees. In total, 114 retention trees were selected.

2.2. TreM assessment

TreM data collection was performed by one trained expert (the first author) in March 2023, before leaf flushing. The trunks of 114 trees were carefully examined from the ground to the crown to detect TreMs, using binoculars for the upper parts of the canopy. TreM types were recorded as presence/absence following the classification described by Larrieu et al. (2018): 47 TreM types belonging to 15 groups and seven general forms (Table 1).

For each retention tree, we also recorded species identity and diameter at breast height (DBH). Tree age was determined through dendrochronological analysis, by collecting two tree core samples at 1 m height. All tree ring samples were taken with 2-thread, 5.15 mm diameter increment borers manufactured by Haglöf Sweden®. After being glued onto wooden backing, samples were sanded with 200-, 400-, and 600-grit sandpaper, and ring counts were conducted using a stereo binocular microscope (3–40×). In cases where the pith was missing, the number of missing rings was estimated based on the ring width of the oldest three rings and an estimation of the distance missed by fitting concentric circles printed on transparent film on the core sample (Asherin and Mata, 2001).

The basal area of trees located around the retention trees (hereafter surrounding BA, $m^2 \, ha^{-1}$) was also obtained as a proxy of stand density, since it strongly correlates with canopy cover in this forest type (Korhonen et al., 2007). To do so, we measured the DBH and distance of all trees within a 9 m radius of every retention tree and estimated the BA (Eq. (1)). To discriminate the close proximity effect of the production trees from the general density effect, we calculated basal area (BA) at different distances from the retention tree (3 and 9 m radius).
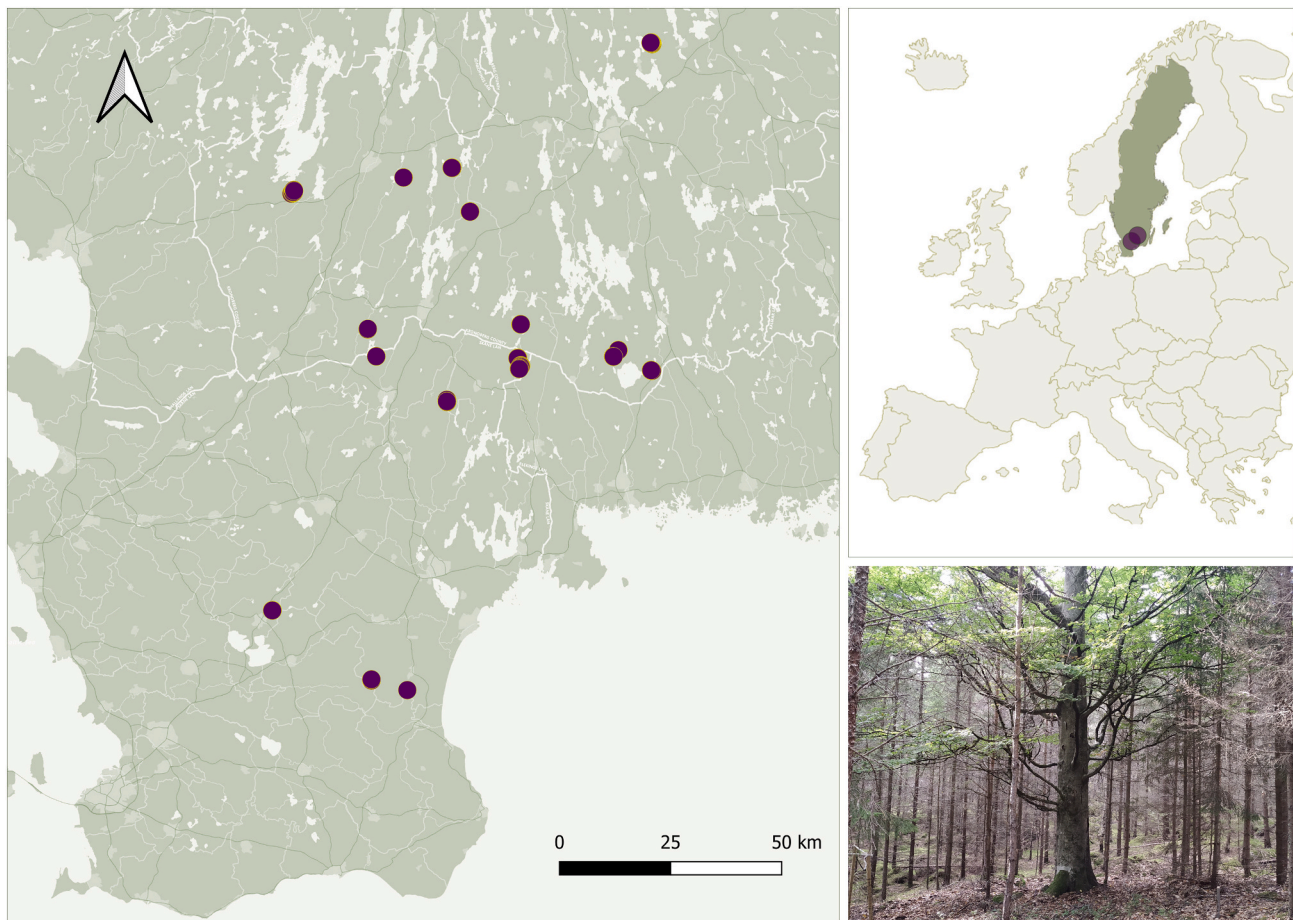
Fig. 1. Location of the production stands studied in southern Sweden and an example of a retention tree (*Fagus sylvatica*) located within a Norway spruce (*Picea abies*) production forest. Foto credit: M.T. Torres-García.

$$BA = \frac{\sum \pi (DBH/2)^2}{\pi r^2} \quad (1)$$

In Eq. (1), *DBH* is the diameter at breast height of all of the trees within the 3 or 9 m radius (*r*) from a retained tree. We assumed the 3 m radius to include surrounding trees directly interfering with the retention tree crowns independently of retention tree size, while 9 m is more important for the general light conditions around the retention tree and its crown. The surrounding BA includes both production Norway spruce trees (approximate 90 %) and broadleaf and smaller conifer trees (10 % approx.).

2.3. Statistical analysis

All statistical analyses were done in R version 4.3.2. We performed a constrained ordination (redundancy analysis, RDA) to evaluate the effects of retention tree species, tree age, and stand density, on TreM type composition, by the *rda* function of the *vegan* package. The RDA was based on the presence/absence of all TreM types occurring at least once and with tree age and stand density as continuous explanatory variables and tree species as factor. Note that the variable tree species refers to aspen, beech, and the taxa birch and oak that include several species (*Betula* spp. and *Quercus* spp.). We carried out a backward selection of explanatory variables with the function *ordistep* from the same package. We selected the variables that best explained the composition of TreMs by dropping non-significant variables to improve the Akaike information criterion (AIC). The function *anova* was used to estimate F-statistics and *P*-values for the full and final models.

To evaluate the effect of retention tree species, tree age, and forest

management on the total diversity of TreM types and groups, and diversity within groups, we used generalized linear mixed models (GLMM) as implemented in the *glmmTMB* function of the package with the same name (Brooks et al., 2017). Stand identity was included as a random intercept factor, due to several trees occurring within the same stand. DBH, retention tree age, retention species identity, stand basal area (at 3 and 9 m radius from the retention trees), and stand age were modelled as fixed effects. We used a Poisson error distribution (log link function) for rot holes, whereas a Conway-Maxwell Poisson distribution (log link function) was used when there was any indication of underdispersion (for overall diversity, concavities, exposed sapwood, exposed sap- and heartwood, crown deadwood and epiphytic structures). Due to the rarity of insect galleries and microsoils, we fitted GLMMs with a binomial error distribution (logit link) on presence/absence data only for these types. Woodpecker breeding cavities (1 observation), twig tangles (6), burrs and cankers (3), ephemeral fruiting bodies (8) and perennial fruiting bodies (2) were excluded from the models for individual TreM groups because of the scarce number of observations. Nests and exudates were not recorded on any tree. To find the best model, we calculated and compared the AICs of the possible models in order to obtain the lowest AIC value. We used the *DHARMa* package for model evaluation by residual plots and dispersion tests. We also performed a variance inflation analysis to exclude variables that can cause multi-collinearity problems (VIF > 2) (Zuur et al., 2010) using the *vif* function of the *car* package and a Spearman correlation analysis using the *cor* function of the *stats* package. The VIF analysis on the full model did not reveal major collinearity problems (Supplementary material Table S1). We quantified the coefficients of determination (conditional and marginal R^2) with the function *r2* in the *performance* package to assess the overall goodness of

Table 1

Classification of TreM types in groups and forms (following Larrieu et al., 2018). Note that only those TreM types observed in this study are shown. Codes before the types correspond to codes in Fig. 2.

Forms	Groups	Types
1. Cavities	1. Woodpecker breeding cavities	WpC: Woodpecker breeding cavities
	2. Rot holes	RH1: Trunk-base rot hole
		RH2: Trunk rot hole
		RH3: Semi-open trunk rot hole
		RH6: Hollow branch
	3. Insect galleries	IG: Insect galleries
	4. Concavities	Con1: Dendrotelm
		Con2: Woodpecker foraging excavation
		Con3: Bark-lined trunk concavity
		Con4: Buttress-root concavity
2. Tree injuries and exposed wood	5. Exposed sapwood only	ESap1: Bark loss
		ESap3: Bark shelter
		ESap4: Bark pocket
	6. Exposed sapwood & heartwood	ESH1: Stem breakage
		ESH2: Limb breakage
		ESH3: Crack
		ESH5: Fork split
3. Crown deadwood	7. Crown deadwood	CD1: Dead branches
		CD2: Dead top
		CD3: Remnants of a broken limb
4. Excrescences	8. Twig tangles	Esho: Epicormic shoots
	9. Burrs & cankers	Bur: Burr
		Can: Canker
5. Fruiting bodies of saproxylic fungi and slime moulds	10. Perennial fungal fruiting body	PF: Perennial fruiting body
	11. Ephemeral fungal fruiting bodies and slime moulds	EF1: Annual polypore
		EF2: Pulpy agaric
		EF3: Pyrenomycete
6. Epiphytic and parasitic crypto- & phanerogams	12. Epiphytic and epixylic structures	Epi1: Bryophytes
		Epi2: Foliose and fruticose lichens
	13. Microsoils	MS1: Bark microsoil
		MS2: Crown microsoil

fit of the model.

3. Results

The mean estimated age of the 114 retention trees was 97 years and their mean DBH was 40.3 cm (Table 2). We found on average 4.2 TreM types per retention tree. Oak had more than five types on average per tree, and up to 10 types in one tree (Table 2). The other tree taxa (aspen, beech, and birch) had between three and four TreM types per tree on average.

We observed 31 different TreM types on the retention trees that belong to 13 out of 15 TreM groups (Table 3). Epiphytes, crown deadwood, and concavities were the most abundant TreM groups, being present in 81, 68, and 42 % of the trees respectively. In contrast,

Table 3

Mean diversity of TreM types (by group) per retention tree species and relative occurrence (%) of TreM groups.

TreM groups	Aspen	Beech	Birch	Oak	Relative occurrence
	(Mean number of TreM types per tree)				(Percentage, %)
1. Woodpecker breeding cavities	0	0	0.04	0	0.9
2. Rot holes	0.55	0.28	0.50	0.77	38.6
3. Insect galleries	0.27	0.04	0.15	0.39	18.4
4. Concavities	0.45	0.50	0.54	0.39	42.1
5. Exposed sapwood only	0.27	0.43	0.27	0.26	28.9
6. Exposed sapwood and heartwood	0.18	0.22	0.31	0.42	26.3
7. Crown deadwood	0.82	0.65	0.73	2.03	68.4
8. Twig tangles	0.09	0.09	0.04	0	5.3
9. Burrs and cankers	0	0	0.08	0.13	1.8
10. Perennial fungal fruiting bodies	0	0.04	0	0	1.8
11. Ephemeral fungal fruiting bodies	0.09	0.07	0.08	0.06	7.0
12. Epiphytic and epixylic structures	0.55	1.24	0.85	0.93	80.7
13. Nests	0	0	0	0	0
14. Microsoils	0	0.28	0.04	0.32	21.1
15. Fresh exudates	0	0	0	0	0

woodpecker breeding cavities, twig tangles, burrs and cankers, ephemeral and perennial fruiting bodies were only rarely found, while no nests or fresh exudates were observed on any retention tree.

The RDA showed that the composition of TreM types on retention trees was significantly related to the species identity, the age of the retention trees, and the surrounding basal area (Fig. 2 and Supplementary material Table S2). Together these variables explained 17 % of the variation in TreM composition (Table S3) with 8.7 % on the first axis, 4.5 % on the second, and the remaining on the other axes. Aspen and birch had similar composition of TreM types (according to their 95 % confidence intervals), but oak and beech clearly differed from each other as well as from aspen and birch in their TreM type composition (Fig. 2). Dead branches (CD1), trunk rot holes (RH2), and insect galleries (IG) were positively correlated to increasing retention tree age and the basal area surrounding the tree (3 m). In addition, abundance of crown microsoils (MS2), exposed sap- and heartwood from limb breakage (ESH2) and dead top (CD2) were positively correlated to the surrounding basal area in a 9 m radius. Whereas the occurrence of bryophytes (Epi1) can benefit from higher stand density, the occurrence of lichens (Epi2) was negatively correlated to density (Fig. 2).

The main drivers of the overall diversity of TreM types and groups were retention tree age and surrounding basal area (Table 4). TreM diversity increased significantly with increasing retention tree age and the basal area of surrounding trees in a 9 m radius. Most groups of TreMs increased significantly with increasing retention tree age, whereas concavities and exposed sap- and heartwood were also promoted by basal area (9 m radius). Higher basal area in close proximity of the retention tree (3 m radius) was positively related to insect gallery abundance whereas it showed a negative effect on concavities. Additionally, tree species was key to explaining the abundance of two TreM
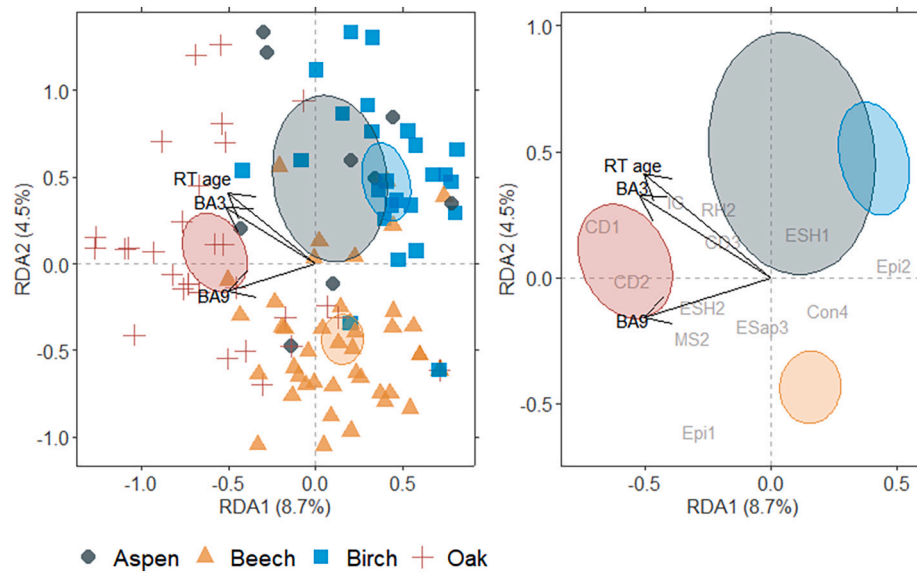
Table 2

Summary of the main characteristics of the retention trees by species and mean and maximum diversity of TreM types and groups per tree ($\pm$ standard deviation).

Species	N. trees	Age (years)	DBH (cm)	Height (m)	Diversity of types		Diversity of groups	
		Mean	Mean	Mean	Mean	Max	Mean	Max
Aspen	11	91.7 ± 16.7	37.9 ± 10.5	20.3 ± 2.47	3.3 ± 2.0	6	3.0 ± 1.8	5
Beech	46	88.1 ± 22.6	39.8 ± 10.0	19.6 ± 3.9	3.8 ± 2.0	9	3.2 ± 1.7	8
Birch	26	99.2 ± 27.7	37.9 ± 8.7	20.0 ± 3.3	3.6 ± 1.7	7	3.2 ± 1.6	6
Oak	31	111.7 ± 25.1	44.1 ± 15.6	20.7 ± 3.7	5.6 ± 2.1	10	4.1 ± 1.5	7
TOTAL	114	97.57 ± 26.0	40.3 ± 11.9	19.8 ± 3.6	4.2 ± 2.2		3.4 ± 1.7	

Fig. 2. Ordination plots from the final RDA model showing the two first ordination axes with the constrained variation in the axes' titles. The left panel represents the complete bidimensional space and the right panel shows the detailed TreM type distribution (non-overlapping). Symbols and colors refer to individual retention trees from different taxa and ellipses represent 95 % confidence intervals around the taxa centroids in ordination space. The grey terms in the right-hand panel refer to the type of TreM. We only display those TreMs with high goodness of fit (see Supplementary material Table S4): RH: Rot holes; IG: insect galleries; Con: Concavities; ESH: Exposed sap- and heartwood; CD: Crown deadwood; Epi: Epiphytes; MS: microsoils (find codes for detailed TreM types in Table 1). The arrows represent significant explanatory variables (RT_age: retention tree age; BA3 and BA9: basal area at 3 and 9 m radius around the retention tree, respectively).

Table 4

Results from generalized linear mixed models (GLMM) after model selection indicating the model coefficients and *P*-values of the predictors (in brackets), and the goodness of the fit (marginal R^2). Significant ($P < 0.05$) predictors are shown in bold. DBH: diameter-at-breast-height, RT Age: retention tree age, BA: basal area. The results from the full model are shown in Table S5 of the supplementary material.

	Intercept	DBH	RT age	Stand age	Surrounding BA		Retention tree species				R^2
					9 m	3 m	Beech	Birch	Oak		
TreM type diversity[a]	0.096	–	**0.007 (<0.001)**	0.007(0.63)	**0.014 (0.004)**	–	0.090	-0.104	0.193	(0.145)	0.106
TreM group diversity[a]	0.204	–	**0.007 (<0.001)**	-0.002 (0.893)	**0.014 (0.001)**	–	–	–	–		0.086
2. Rot holes[b]	-2.350	–	**0.020 (<0.001)**	-0.027(0.60)	–	0.017(0.071)	–	–	–		0.228
3. Insect galleries[c]	-4.777	–	0.019(0.085)	–	–	**0.073 (<0.001)**	–	–	–		0.260
4. Concavities[a]	-0.622	–	0.006(0.127)	-0.041 (0.341)	**0.031 (0.009)**	**-0.025 (0.020)**	–	–	–		0.233
5. Exposed sapwood[a]	-2.530	–	**0.017(0.029)**	-0.013 (0.820)	–		0.576	-0.570	-0.399	(0.064)	0.309
6. Exposed sap- and heartwood[a]	-2.165	–	**0.014(0.038)**	-0.050 (0.438)	**0.032 (0.038)**	–	–	–	–		0.336
7. Crown deadwood[a]	-1.374	–	**0.005(0.041)**	0.028 (0.269)	–	**–**	**-0.326**	**-0.241**	**0.721**	(**<0.001**)	0.501
12. Epiphytic structures[a]	-1.269	0.001 (0.067)	-0.001(0.689)	0.048 (0.069)	-0.013 (0.115)	–	**0.793**	**0.649**	**0.852**	(**0.047**)	0.311
14. Microsoils[c,d]	-3.339	–	0.009(0.494)	0.055 (0.605)	–	–		-2.201	-0.307	(0.054)	0.212

[a] Conway-Maxwell Poisson distribution.

[b] Poisson distribution.

[c] Binomial distribution.

[d] Model without observations from aspen trees due to zero observations of microsoils in this tree species.

groups: crown deadwood and epiphytic structures. Particularly, crown deadwood was significantly more abundant in oaks than in other retained tree species. Even though stand age was included in most of the models (nine out of ten), this variable never had a significant effect on TreMs.

4. Discussion

4.1. Broadleaf retention trees as a key source of TreMs

Broadleaf retention trees in even-aged conifer-dominated hemi-boreal production forests can develop at least 31 different types of TreMs from 13 groups, which on average was 4.2 types of TreMs per tree. Our results therefore highlight, for the first time, the important contribution that retention trees can make to the provision of TreMs within early

rotation (approx. 30 years of age) intensively managed production forests in a hemiboreal context. However, we observed that the composition and diversity of TreMs was driven by the species of retention tree, its age, and the density of trees (mostly production conifers) surrounding the retention trees.

There is a growing body of evidence that tree species identity influences the general abundance of TreMs, as well as the occurrence of particular TreM assemblages (e.g., Courbaud et al., 2022). These differences can be related to tree specific features such as bark type, compartmentalization capacity of wounds, and phyllotaxis (Larrieu et al., 2022), but also on successional status and light demands of the tree species (Courbaud et al., 2022). We found that aspen and birch trees, which are pioneer and shade-intolerant species, shared a similar composition of TreM types. Conversely, beech trees (late-successional and shade-tolerant species) showed a different assemblage of TreMs that also differed from the late-successional but shade-intolerant oaks. Moreover, oaks have a higher wound compartmentalization capacity compared to beech, aspen and birch (Gilman, 2011), which is related to the physical and chemical properties of the wood (Smith, 2015). Although our dataset is too limited to derive generalized conclusions, our results nevertheless open up a new avenue for research since TreM diversity has very scarcely been explored using this type of inter-trait comparison. The speed of TreM development (formation rate) and the periods of tree growth when TreMs appear (hazard rate) has been analyzed among species with contrasting life-history traits (Courbaud et al., 2022; Spînu et al., 2023). Spînu et al. (2023) observed that short-lived pioneer species developed TreMs quicker than long-lived species (but see Courbaud et al., 2022). Since investing in the defense against pathogens is a compromise with growth speed and lifespan (Loehle, 1988), fast-growing and short-lived pioneer broadleaves generally have low compartmentalization capacity because their investment in defense barriers is very low (Morris et al., 2016). In this regard, Larrieu et al. (2021) showed a significant effect of successional status for several co-occurrences of TreMs.

In our study, the longer-lived oaks had a high diversity of TreM types, which is in line with Vuidot et al. (2011) that highlighted the importance of oaks as TreM-rich tree species. Oaks are commonly selected as retention trees in the hemiboreal zone because of their high biodiversity value (Koch Widerberg et al., 2012), as well as their long potential life spans that can exceed 500 years in southern Sweden (Drobyshev and Niklasson, 2010). However, oak vitality can be severely affected by forest management, as oaks, especially *Q. robur* and *Q. petraea*, are light-demanding tree species (Larsen et al., 2005). In fact, we observed that oaks had the highest occurrence of crown deadwood, which can be related to the dense and shady conditions occurring within conifer-dominated production forests. In this context, in which retained oaks are often surrounded by dense forest conditions, their lifespan can be curtailed (Lariviere et al., 2021). Despite the fact that dead trees can provide even more TreMs than living ones (Vuidot et al., 2011), the longer these trees survive, the longer they will provide TreMs for forest biodiversity (Fritz and Heilmann-Clausen, 2010).

Making allowances for the longer-term survival of these trees is especially crucial for the development of rot holes and their associated communities. Oaks, as well as aspens, developed the highest diversity of rot holes but also of insect galleries (Table 3). Aspen is a common tree species in boreal and hemiboreal regions and is also known to be an important cavity-bearing tree (Andersson et al., 2018; Remm and Lõhmus, 2011). Our results indicate that by promoting different retention tree species, an array of different TreMs may be increased in production forests. Tree species such as oaks can be actively selected for as retained trees, even prior to the development of TreMs, as the probability of future TreM formation can be higher than other tree species (Courbaud et al., 2022). In the meantime, pioneer species such as birch and aspen can be also targeted since they can develop TreMs quicker than longer-lived species such oaks (Spînu et al., 2023), and their limited lifespan provides shorter time periods to deadwood provision; which is

another old-growth-forest attribute essential for biodiversity (Bauhus et al., 2009).

4.2. Old trees host higher diversity of TreMs

Tree age was the main driver of the diversity of TreM types and groups on retention trees. To our knowledge, there is only one previous study (Kozák et al., 2023) that analyzed the relationship between tree age and TreM occurrence and diversity. We observed that as tree age increased, the overall diversity of TreM types significantly increased, as well as the occurrence of some TreM groups, including rot holes, crown deadwood, exposed sapwood only and exposed sap- and heartwood. This can be explained by the longer time frame needed to develop these groups of TreMs and the increasing susceptibility of individual trees to the age-related abiotic and biotic damages that underlie their formation (Kozák et al., 2023). Crown deadwood is a TreM strongly associated with ontogenic stages of maturity and senescence (Larrieu et al., 2022), whereas rot holes originate from bark losses. It is likely that the use of skidders and other equipment during logging promoted the bark lost in the retained trees first, which later derived into the observed rot holes through a saproxylation process that can take between 10 and 20 years just to reach a first stage in the cavity development, depending on tree species, fungi, and insects that colonize the bark. As a result, the older the trees are, the more likely they are to create these slow-developing TreMs (Fritz et al., 2009; Kozák et al., 2023; Ranius et al., 2009).

Tree diameter is commonly used as an indirect measure of tree age (Asbeck et al., 2019; Larrieu and Cabanettes, 2012; Michel and Winter, 2009; Winter and Möller, 2008) since it is faster and easier to measure, especially for forest managers that record DBH routinely (Larrieu et al., 2018). However, as observed in our study, tree age and diameter are not always strongly correlated (Fig. S6), as this relationship is highly dependent on the tree species and their environmental context (Larrieu et al., 2022). In particular, long-lived and shade-tolerant species such as yew (*Taxus baccata*), silver fir (*Abies alba*), and beech can grow more slowly with increasing age, relative to other tree species (Pavlin et al., 2021). More specifically, these species are able to reduce their growth rates significantly during extended periods of time (e.g., decades) when there is insufficient light, and then resume higher rates of growth when the light environment improves. In such cases, the correlation between DBH and tree age can be very weak. The potential lack of a correlation between tree size and age is particularly relevant to the context of our study, as the retention trees must compete with adjacent fast growing conifer trees for both light and resources, but also in mixed and primary forests where suppressed trees can decrease their growth rates (Kozák et al., 2023; Pavlin et al., 2021). We directly estimated tree age using dendrochronology, which enabled us to include tree age in all of the selected models that accounted for the diversity of TreM types and groups. DBH was only maintained as an explanatory variable, although not significant, when considering epiphytic structures. Although more difficult to obtain than DBH, retention tree age seems to have a stronger explanatory power of TreM type diversity and our results emphasize the relevance of age when predicting TreM occurrence, particularly in long-lived retention trees. In addition, the use of tree age will improve TreM research by making studies more comparable across forests spanning contrasting regions and management regimes.

Despite the occurrence of old retention trees in our study, many of the trees may not have been old enough for the formation of some TreMs, such as woodpecker breeding cavities or nests (Paillet et al., 2017). We are aware of the limitations of our dataset and that the absence of some TreM types should be interpreted with caution. However, it is known that some TreMs such as woodpecker foraging excavations, cracks, and fruiting bodies are much less frequent on living trees (Larrieu and Cabanettes, 2012). The presence of snags, especially large ones, in production forest monocultures with retention trees is limited, which likewise limits the occurrence of TreM types associated with dead and dying trees, and their associated biodiversity.

4.3. Forest management effects on TreM diversity

Whereas production-orientated forest management often aims for short rotation periods, retention trees act as a partial compensatory measure that promotes old-growth attributes such as TreMs (Gustafsson et al., 2020a). The contrast between the production and conservation goals of the two categories of trees raises the potential for important interactions to take place between retention and production trees that can dictate the resultant occurrence of TreMs in production forests. For example, the basal area of the production trees that surround the retention tree – which is largely an outcome of silvicultural management decisions, site fertility, the production tree species itself, and stand age – can affect the general abundance and diversity of TreMs (Fan et al., 2003; Slater, 2018; Winter et al., 2015). In a retention forestry context, we found that the overall diversity of TreM types, as well as particular types such as insect galleries, concavities, and exposed sap- and heartwood, were likewise associated with surrounding basal area. It is likely that a high density of surrounding trees promoted TreMs such as dead branches and consequently, branchless trunks in retention trees, increasing the susceptibility to cavity formation (Larrieu et al., 2022). We are aware that TreMs can develop over a long-time frame, and the current basal area reflects the latest stage in the life of the retention tree. However, TreM types such as bryophytes and lichens which are more ephemeral, have been shown to be positively and negatively affected by surrounding tree density respectively. These results may reflect the contrasting physiological niche of these epiphytic species (Asbeck et al., 2019); many forest bryophytes prefer shady wet conditions whereas lichens can often be more light demanding. Although the GLMM did not show a density effect on epiphytic structures, that is the TreM group that gather both bryophytes and lichens, the RDA did reveal such a pattern. Therefore, production tree density can have both positive and negative effects on the occurrence of specific TreM types, as well as on the vitality and lifespan of some retention tree species.

4.4. Biodiversity implications and practical recommendations

We found that broadleaf retention trees can develop a high diversity of TreMs in the intensively managed production forests of the hemiboreal region. The high TreM diversity we observed may in-turn indicate high TreM-related biodiversity, at least according to the habitat heterogeneity hypothesis, which states that higher stand complexity will contribute to higher species number (Tews et al., 2004). Old retention trees, and particularly oaks, appear to be well suited to the development of a high diversity of TreMs, particularly rot holes that can have a key role as habitat for epiphytes, saproxylic insects (Fritz and Heilmann-Clausen, 2010; Müller et al., 2014), and as roosting sites by bats (Ruczyński and Bogdanowicz, 2005). The occurrence of lichens, which can be essential habitat for mollusks, arachnids, Coleoptera, and Lepidoptera (Bütler et al., 2020), was negatively related to production stem density. However, the reduced occurrence of lichens may be countered by the fact that the proximity and density of production stems was associated with the increased occurrence of both insect galleries, which are used by cavity dwellers for feeding (Paillet et al., 2018), and crown deadwood which host specific assemblages of saproxylic fungi and beetles (Bouget et al., 2011; Ellis and Ellis, 1998). Therefore, some retention tree species (e.g. shade-intolerant oaks) could benefit from reducing surrounding tree density, which will increase their life-span (Larivière et al., 2021) without compromising their capacity to provide an array of TreM types for multiple taxa. In contrast, shade-tolerant tree species such as beech can tolerate denser forest conditions and promote those TreMs associated with a higher density of surrounding trees.

Overall, our results support the contribution of broadleaf retention trees to the establishment and conservation of TreMs in intensive production forests found in a hemiboreal region. The diversity of TreM types we observed (4.2 per tree) was similar to the diversity observed in central Europe, where tree retention occurred within production forests managed using continuous-cover forestry (Asbeck et al., 2019). Retained beech trees in particular showed a similar diversity of TreM types (3.8 per tree) to beech trees found in the mixed conifer-broadleaf forests of Germany (3.6 TreMs per tree, Asbeck et al., 2019). However, we observed a higher diversity of TreM groups in our production context compared to what is reported on some production stands of central Europe with similarly sized or even larger habitat trees (Asbeck et al., 2020, 2019; Spînu et al., 2022). Since the number of retention trees is usually scarce in intensively managed production forests (approximately 10 retention trees required per hectare by FSC certification in Fennoscandia (Forest Stewardship Council, 2020)), TreM density at stand level can be expected to be boosted with increasing levels of retention of habitat trees (Bütler et al., 2013) as well as with the promotion of snags that contribute to different assemblages of TreMs (Larrieu and Cabanettes, 2012; Paillet et al., 2019). In this sense, further research is needed to unveil the effects of both retention tree density and snags on TreM occurrence in even-aged conifer-dominated production forests.

CRediT authorship contribution statement

M. Trinidad Torres-García: Writing – original draft, Methodology, Investigation, Formal analysis, Data curation, Conceptualization, Writing – review & editing. **Per-Ola Hedwall:** Writing – review & editing, Methodology, Formal analysis, Conceptualization. **Laurent Larrieu:** Writing – review & editing, Methodology. **Erik Öckinger:** Writing – review & editing, Conceptualization. **Henrik Johansen:** Investigation. **Mats Niklasson:** Writing – review & editing, Investigation. **Lisa Petersson:** Writing – review & editing, Investigation. **Emil Svensson:** Writing – review & editing, Investigation. **Jaime Uría-Díez:** Writing – review & editing, Investigation, Conceptualization. **Adam Felton:** Writing – review & editing, Funding acquisition, Conceptualization.

Declaration of competing interest

There are no conflicts of interests to declare.

Acknowledgements

Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.biocon.2024.110821.

Data availability

Data will be made available on request.

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