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Influence of individual tree characteristics, spatial structure and logging history on tree-related microhabitat occurrence in North American hardwood forests

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Abstract

Background: Tree-related microhabitats (hereafter, “TreMs”) are key components of forest biodiversity but they are still poorly known in North American hardwood forests. The spatial patterns of living trees bearing TreMs (hereafter, “TreM-trees”) also remain to be determined. As logging practices can lead to a loss of TreM-trees and of their associated biodiversity, it is essential to identify the factors explaining TreM occurrence to better integrate them into forest management. We therefore inventoried TreMs in 4 0.5-ha survey strips in northern hardwood forests in Quebec, Canada, while recording the spatial location of each tree. Two strips were located in unmanaged old-growth forests, and 2 were in forests managed under selection cutting. All 4 stands were dominated by sugar maple (*Acer saccharum* Marsh.) and American beech (*Fagus grandifolia* Ehrh.). Beech bark disease, an exotic pathology, was observed in all the strips.

Results: Large diameter at breast height and low tree vigor were the main characteristics explaining the presence of TreMs at the tree scale. TreM-trees presented slight spatial aggregation patterns. These aggregates, however, were not well-defined and were generally constituted by a large number of trees bearing few different types of TreMs. Two TreM classes (broken branch or top and woodpecker lodge) also presented a spatial aggregation. Logging practices had no significant effect on TreM occurrence. Beech bark disease increased the frequency of senescent beeches. The impact of this pathology on TreMs was however mitigated by the small size of infected trees and probably by the short time elapsed since its appearance.

Conclusion: The factors explaining the presence and abundance of TreMs on trees has so far been little studied in North American hardwood forests. Our results highlight that TreM-tree characteristics in the surveyed forests are consistent with those of previous studies conducted in other forest types and regions (e.g., Europe or Northwestern America). To our knowledge, this study is also the first to identify a spatial aggregation of TreM-trees and of specific TreM classes. It will be nevertheless necessary to determine whether the small impact of logging activities we observed results from current or past management practices.

Keywords: Habitat trees, Wildlife habitat, Northern hardwoods, Old-growth forest, Selection cutting, Ecosystem-based management, Biodiversity indicators, Conservation, Forest management

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Background

Finding a balance between wood production and other ecosystem services, such as biodiversity, carbon sequestration or aesthetic values, is now a common objective of forest management (Sarr and Puettmann 2008; Puettmann et al. 2009; Watson et al. 2018). For this purpose, many silvicultural practices that mimic natural forest dynamics have been proposed. These strategies for sustainable forestry include maintaining continuous forest cover, complex horizontal and vertical forest structure, large trees, as well as standing or fallen deadwood (Bauhus et al. 2009; Raymond et al. 2009; Eyvindson et al. 2021). However, evaluating the capacity of actively managed forest landscapes to maintain structural attributes and biodiversity close to that of natural forests is challenging. Exhaustive biodiversity surveys are often hard to implement, expensive and generally concentrated on a few taxa (Puimalainen et al. 2003; Burrascano et al. 2018; Larrieu et al. 2019). Accordingly, proxies of forest biodiversity are generally preferred in lieu of exhaustive surveys (Burrascano et al. 2018; Larrieu et al. 2018a; Larrieu et al. 2018b; Barrette et al. 2020).

Tree-related microhabitats (hereafter “TreMs”) are among the proposed indicators that can help to better identify the structural elements supporting forest biodiversity (Larrieu et al. 2018a; Asbeck et al. 2021). They are defined as “*all distinct and well-delineated structures occurring on living or standing dead trees, that constitute a particular and essential substrates or life site for species or species communities during at least a part of their life cycle to develop, feed, shelter or breed*” (Larrieu et al. 2018a). Examples of TreMs include cavities, broken branches or trunks, and fruiting bodies of saproxylic fungi that harbor specific animal, vegetal and fungal species (Bouget et al. 2013; Regnery et al. 2013; Larrieu et al. 2018a; Paillet et al. 2018; Basile et al. 2020). TreM surveys are easier to conduct than complete censuses of species richness and diversity (Larrieu et al. 2018a). For example, Martin and Raymond (2019) showed that they could be easily identified at the same time as tree-defect inventories, which are common in temperate managed forests.

Research considering the concept of TreMs as structural and functional resources for a wide range of taxa is scarce in North America, and most of the current knowledge is built on studies from temperate, Mediterranean and mountain forests of Europe (Larrieu et al. 2018a). The majority of the existing research in North America comes from the West Coast (Stevenson et al. 2006; Michel and Winter 2009; Michel et al. 2011; Pritchard et al. 2017; Asbeck et al. 2020a). On the East Coast, the few existing studies on TreMs were performed either on urban trees compared to trees in natural hardwood

forests (Großmann et al. 2020), in the conifer-dominated boreal forest (Martin M, Fenton NJ, Morin H: Tree-related microhabitats and deadwood dynamics form a diverse and constantly changing mosaic of habitats in boreal old-growth forests, submitted) or in the temperate mixedwood forest (Martin and Raymond 2019), the latter marking the transition from boreal to temperate forests. In terms of management guidelines, TreM-trees are almost exclusively those with cavities and other TreMs are rarely considered (Ontario Ministry of Natural Resources (OMNR) 2004; Ministère des Forêts de la Faune et des Parcs (MFFP) 2017). Therefore, better knowledge of the full range of tree microhabitats in temperate hardwood forests is needed to set the standards for maintaining their diversity and abundance in managed forests.

In Europe and western North America, studies highlighted that a larger diameter at breast height (DBH) and a lower tree vigor are the main characteristics explaining the presence of numerous and/or large TreMs (Vuidot et al. 2011; Winter et al. 2015). It is thus likely that the same factors will drive TreM formation in temperate forests of eastern North America. Yet, little is known about the spatial arrangement of TreM-trees (i.e., tree bearing at least one TreM), for example, if they are spatially clumped or, on the contrary, dispersed. As TreMs often result from abiotic or biotic damages (e.g., wind damage, fall of a dead tree or branch, fungal infection, insect epidemics), a distinct spatial pattern of TreM-trees has been expected (Kozák et al. 2018; Asbeck et al. 2020b), but has been observed only for woodpeckers cavities (Puverel et al. 2019). Understanding the spatial structure of TreMs is, nonetheless, a key factor in developing sustainable silvicultural practices aiming to maintain biodiversity in managed forests. Innovative silvicultural systems for example aim to increase the horizontal complexity of forest stands by combining the creation of various-sized gaps and the selection of individual trees (Kane et al. 2011; Bédard et al. 2014; Raymond et al. 2018). Knowing the spatial patterns of TreM-trees would help to maintain patches of habitat trees and to ensure that they act as effective ecological corridors for taxa with low dispersal capacity. Yet, silvicultural practices can have a negative impact on TreMs. According to European studies carried out in hardwood or mixedwood temperate forests, silvicultural practices generally cause a loss of TreM abundance and diversity, because (i) trees considered as senescent or with lower wood quality are progressively removed, and (ii) trees are often harvested before they can reach a diameter that favor the development of TreMs (Winter and Möller 2008; Larrieu et al. 2012; Larrieu et al. 2014; Paillet et al. 2017). The impacts of silviculture on TreMs must therefore be evaluated in terms of density, diversity and general composition.

In this study, we aim to identify the factors promoting TreM development on living trees in hardwood temperate forests of eastern North America. Selection cutting, i.e. the harvest of trees of multiple sizes to create gaps, is a silvicultural practice common in these forests. We predicted that in unmanaged old-growth forests, a combination of tree characteristics (large diameter at breast height, low tree vigor) and of spatial variables (spatial aggregation) increases the probability that a tree develops TreMs. Moreover, we expect that selection cutting will create a more uniform spatial arrangement of TreM-trees, as these would be logged first to promote healthy and/or valuable trees at a more or less regular spacing to optimize wood production.

Material and methods

Study area

The study was conducted in the Papineau-Labelle Wildlife Reserve (45°59' N, 75°20' W), a 162,800 ha territory landscape in the sugar maple (*Acer saccharum* Marshall)–yellow birch (*Betula alleghaniensis* Britton) bioclimatic ecoregion (Saucier et al. 2009) in western Quebec, Canada (Fig. 1). Mean annual temperatures range from 2.5 °C to 5 °C, precipitations from 900 to 1100 mm, and the growing season lasts from 170 to 180 days (Gosselin 2002). The topography is essentially characterized by hills with gentle slopes. Sugar maple and yellow birch are the dominant tree species. Other species such as American beech (*Fagus grandifolia* Ehrh.), white birch (*Betula papyrifera* Marshall), red maple (*Acer rubrum* L.), or balsam fir (*Abies balsamea* (L.) Mill.) can also be found (Gosselin 2002). Most of the forests in this region have been actively managed since the early twentieth century (Gaffield 1994). The forest was harvested by selective cutting practices such as diameter-limit cutting, i.e., the harvest of healthy trees that reached a specific diameter, until selection cutting, i.e., the harvest of trees of multiple sizes to create small gaps, became prevalent in the years 1990s (Bédard et al. 2014; Lussier and Meek 2014; Nyland 2016). The most notable exception is the Lac-de-l'Écluse forest (45°52' N–75°24' W), one of the largest landscapes (7.74 km²) of hardwood old-growth forest found in Quebec. This protected area is considered as an old-growth forest because (i) it has not been severely affected by natural disturbances since several centuries and (ii) present no traces of forest management since the European settlement in this region (Ville-neuve and Brisson 2003). The influence of First Nations on North American forests prior to this time was essentially forest fires (Munoz and Gajewski 2010; Blarquez et al. 2018). Beech bark disease (BBD) is an exotic pathology that has been present in the study territory at least since 2013 and currently causes a marked senescence and mortality of beech trees (Morin et al. 2007; Ministère des Forêts de la Faune et des Parcs (MFFP) 2020).

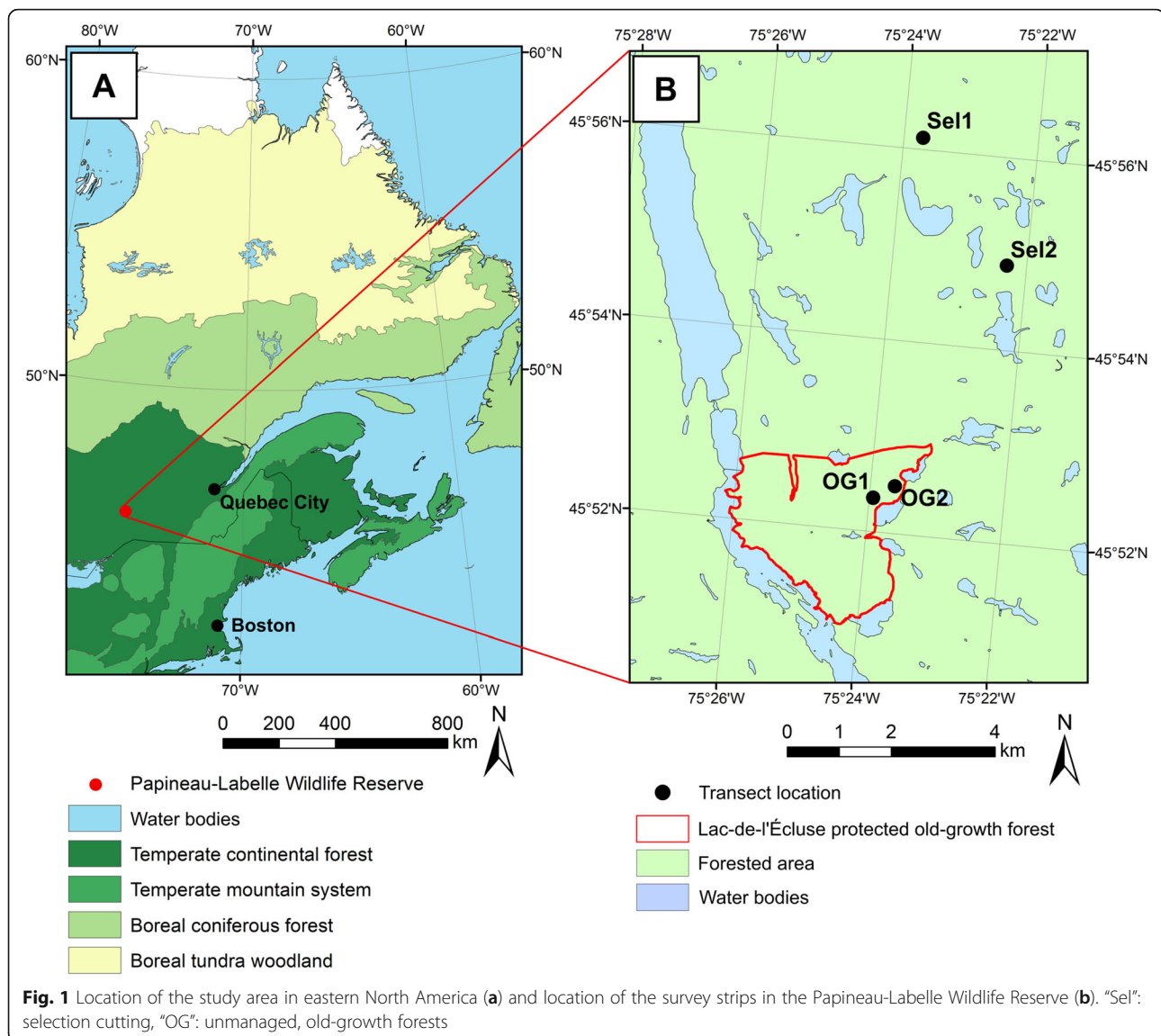
Sampling design and strip characteristics

In 2014, we set up two survey strips (0.5 ha each, 500 m-long, 10 m-wide) in managed forests (named “Sel1” and “Sel2”) and 2 others of the same size in the Lac-de-l'Écluse old-growth forest (named “OG1” and “OG2”; Fig. 1). Their location was determined using stratified random sampling, based on five variables defining forest tree species composition, successional stage and history: (i) potential vegetation (namely, the theoretical tree composition at the end of the succession, here a sugar maple–yellow birch forest); (ii) stand structure (irregular and older than 80 years based on the provincial forest survey age and structure typology (Ministère des Ressources Naturelles et de la Faune du Québec (MRNF) 2008)); (iii) logging history (logged or unlogged, that is to say, within the Lac-de-l'Écluse old-growth forests); (iv) distance from forest road (at most, 125 m to avoid any edge effect); and (v) size sufficient to survey a 500 m-long strip following a cardinal point without encountering any change in potential vegetation or edge effect.

Each strip was delimited using hip chain and measuring tape, and by aiming a compass at 1 of the 4 cardinal points. When we crossed a tree with a DBH \geq 19 cm within the strip limits (i.e., at most 5 m from the center of the strip), we recorded its species, DBH, vigor class (vigorous, senescent (with a low probability of survival according the tree vigor classification scheme of Boulet (2005)) or dead (snag)), location within the strip and the occurrence of TreMs (presence/absence, on living trees only). When these were present, we noted the TreM classes (Table 1) adapted from Emberger et al. (2013). We considered the centroid of the trunk at breast height along the north/south and east/west axes as the exact location of the tree within the strip. We sampled a total of 366 living trees and 58 snags.

Statistical analyses

To assess our prediction that a combination of environmental and spatial variables increases the probability of a tree developing TreMs, we first performed a Bayesian generalized linear mixed effects model (GLMM) with a Poisson distribution for count data (hereafter, “Poisson GLMM”), based on the attributes of surveyed living trees and using the *bglmer()* function of the *blme* package (Chung et al. 2013) in R software (R Core Team 2019). We decided to use a mixed-effect model to limit the influence of the spatial links that might exist between trees in a same transect and that can influence models' reliability (Dormann et al. 2007). The random effect consisted therefore of the nested transect with the forest management status (managed under



selection cutting or old-growth; hereafter “Management”), similarly as previous research studying TreMs (e.g., Paillet et al. 2019; Asbeck et al. 2020b). The Bayesian approach was chosen to avoid model singularity (i.e., variances of one or more linear combinations of effects are close to zero), as suggested by Bates et al. (2015), using a covariance matrix of the random effects based on the Wishart distribution (Chung et al. 2013). The dependent variable was the total number of TreM-classes on the tree, and the independent variables were tree DBH, tree vigor, management and number of TreM-trees among the five closest living trees (“TreM-trees aggregation”). We used the function *step()* in R software to perform a stepwise selection to obtain the most parsimonious model. The validity of the model (overdispersion, zero-inflation) was assessed using

the *DHARMA* package (Harting 2019). Then, we performed for each TreM class a Bayesian GLMM with a logistic distribution for binary data (hereafter, “Logistic GLMM”), using the same random effects and covariance matrix than the Poisson GLMM. The dependant variable was the presence/absence of the TreM class studied on each tree, and the independent variables the same as the Poisson GLMM. For each model, we also performed a stepwise selection to obtain the most parsimonious model. Validity of the models were verified similarly as before. For each logistic GLMM, we determined its predictive ability using the area under the receiver operating characteristic curve (AUC, Zweig and Campbell 1993), which ranges from 0.5 (uninformative model) to 1 (perfect model; Fielding and Bell 1997).

Table 1 TreM typology adapted from Emberger et al. (2013). ^a: The potential users of the different TreM classes is based on the literature review of Larrieu et al. (2018a)

TreM class	Description	Potential users ^a
Bark loss	At least 600 cm ² of sapwood exposed, with the bark still attached or not	Mammals, birds, gastropods, insects, fungi
Broken branch or top	Broken branch or top with a diameter \geq 20 cm at the broken point	Birds, insects, arachnids, fungi, lichens
Crack	Crack with width > 1 cm and depth > 10 cm	Mammals, birds, gastropods, insects, arachnids, fungi, lichens
Crown deadwood	At least 20% of the crown is dead or one dead branch with length > 1 m and diameter > 20 cm	Birds, insects, arachnids, fungi, lichens
Saproxyllic fungi	Fruiting bodies > 5 cm in diameter or occur in 10 cm long cascades of smaller fruiting bodies	Gastropods, insects, arachnids, bryophytes, fungi
Trunk base rot hole	Diameter > 10 cm, direct contact with the ground	Mammals, birds, amphibians, insects, arachnids, bryophytes, fungi, lichens
Trunk rot hole	Diameter > 10 cm, no contact with the ground, on the trunk or on a branch	Mammals, birds, amphibians, insects, arachnids, bryophytes, fungi, lichens
Woodpecker cavity	Any cavity initially carved by a woodpecker for nesting. Feeding cavities are excluded	Mammals, birds, amphibians, insects, arachnids, bryophytes, fungi, lichens

Tree species was not included in the GLMMs models, as preliminary analyses indicated that this variable was strongly associated with tree vigor because of the BBD. To better understand the influence of tree species in our results, we first analyzed the frequency of TreM-trees (living trees bearing at least one TreM class), TreM classes and tree vigor classes by tree species, using pairwise Fisher tests with a Bonferroni adjustment (Mangiafico 2016). Less common tree species were grouped in a same category ("Other species"). It was sometimes impossible to clearly determine the species of dead trees. Therefore, trees of unknown species were not considered in the Fisher analysis of tree vigor classes. Second, we compared the DBH of living sugar maple and American beech trees using Kruskal-Wallis test, also taking into account the presence/absence of TreMs (sugar maples with TreMs, sugar maples without TreMs, American beeches with TreMs, American beeches without TreMs). If this test result was significant, we then performed Dunn's post hoc test (Dunn 1964) with a Bonferroni correction. Finally, to determine if specific TreM classes tended to be more closely associated with other classes on the sampled trees and if selection cutting maintained specific TreM assemblages, we performed a non-metric dimensional scaling analysis (NMDS) based on the presence/absence of the different TreM classes. The NMDS was followed by an analysis of similarities (ANOSIM; Clarke 1993), with management as the dependent variable, using Jaccard distance and 9999 permutations. Only living trees bearing at least 2 different TreM classes were considered in this analysis.

The analyses were performed on R software, version 3.6.1 (R Core Team 2019), using the *blme* (Chung et al. 2013), *DHARMA* (Harting 2019), *ROCR* (Sing et al. 2005), *Desctools* (Signorell 2017), *emmeans*

(Russel 2018), *FactoMiner* (Lê et al. 2008), *rcompnion* (Mangiafico 2019), *FSA* (Ogle et al. 2019) and *vegan* (Oksanen et al. 2018) packages.

Results

Strip characteristics

The studied strips were dominated by sugar maple, with American beech as the second dominant species (Table 2). Other tree species were present to a lesser, except in the OG1 strip, where the presence of a few large eastern hemlocks (*Tsuga canadensis* (L.) Carrière) and yellow birches explains greater basal area values. The mean DBH of living trees and snag was equal to $34.3 \pm$

Table 2 Structural attributes and composition of trees (defined by a DBH \geq 19 cm) in the studied strips. "Sel": selection cutting, "OG": unmanaged old-growth forests

Attribute	Sel1	Sel2	OG1	OG2
Tree density (n·ha ⁻¹)	210	152	208	162
Tree basal area (m ² ·ha ⁻¹)	22.4	14.3	20.6	19.6
Sugar maple tree frequency (%)	73.3	65.8	86.5	64.2
American beech tree frequency (%)	24.8	28.9	5.7	28.4
Other tree species frequency (%)	1.9	5.3	7.7	7.4
Sugar maple basal area frequency (%)	84.9	78.2	85.9	74.1
American beech basal area frequency (%)	13.5	19.3	2.9	15.1
Other species basal area frequency (%)	1.6	2.5	11.1	10.8
Senescent tree density (n·ha ⁻¹)	30	32	14	36
Senescent tree basal area (m ² ·ha ⁻¹)	3.1	2.3	0.4	2.3
Snag density (n·ha ⁻¹)	24	20	36	34
Snag basal area (m ² ·ha ⁻¹)	3.9	2.5	5.4	5.0
Tree mean DBH (cm)	34.7	32.9	33.2	36.4
Snag mean DBH (cm)	44.7	38.4	42.3	41.9

12.8 cm and 41.9 ± 11.0 cm, respectively. The DBH range in the studied strips was equal to 19–84 cm for the trees and 22–74 cm for the snags.

TreM composition in northern hardwoods

We found that 40% of living trees bore at least one TreM, for a mean density of $72.5 \text{ TreMs} \cdot \text{ha}^{-1}$ (Table 3). TreM-trees were observed in each transects but few trees contained at least 3 different TreM classes (Fig. 2). On average, TreM-trees had 1.49 TreM classes and a mean DBH of 40.4 cm (Table 3). The most abundant TreM classes were bark loss ($30.5 \text{ trees} \cdot \text{ha}^{-1}$) and rot holes (mean density: $26 \text{ trees} \cdot \text{ha}^{-1}$). In contrast, the least abundant TreM classes were cracks (mean density: $3.5 \text{ trees} \cdot \text{ha}^{-1}$) and trunk base rot holes (mean density: $4 \text{ trees} \cdot \text{ha}^{-1}$).

Factors driving TreM occurrence

The Poisson GLMM was significant ($p < 0.001$) and contained three variables, all significant: DBH ($p < 0.001$), tree vigor ($p < 0.001$) and TreM-trees aggregation ($p = 0.006$) (Table 4). The number of different TreM classes observed on the same tree increased significantly with DBH (Fig. 3a). Senescence and a higher agglomeration of TreM-trees also had a positive, although more moderate, effect (Fig. 3b and c). All logistic GLMMs were significant except for bark loss ($p = 0.084$), saproxylic fungi ($p = 0.168$) and trunk base rot hole ($p = 0.172$) (Table 5). For the significant models, we observed high and relatively homogeneous

AUC values (0.74–0.84; Table 4). DBH had a significant positive influence in all final models (Fig. 4a). Tree vigor significantly increased the probability of occurrence of crown deadwood and woodpecker lodge (Fig. 4b). Management had no significant influence on the occurrence of the different TreM classes. We however observed a trend ($p = 0.081$) for crown deadwood, where the occurrence of this class was lower in forests managed under selection cutting (Fig. 4c). Finally, the TreM-trees aggregation positively influenced the occurrence of broken branch or top, as well as woodpecker lodge (Fig. 4d). One tree was removed from these analyses due to unknown tree vigor (number of trees considered in the analyses: 365).

The occurrence of TreMs was not different among species. However, we observed significant differences in the frequency of TreMs and tree vigor classes between sugar maple and American beech (Table 6). Most TreM classes were observed on sugar maple. On American beech, only crown deadwood and saproxylic fungi were very frequent (observed on 40% and 56% of the TreM-trees, respectively), while other classes were infrequent (observed on less than 16% of the TreM trees). Similarly, American beech accounted for 75% of the senescent trees, whereas the majority of the vigorous trees were sugar maples (83% of the vigorous trees). Overall, other tree species presented few differences with sugar maple and American beech. The only significant difference concerned tree vigor, as a higher proportion of beeches were classified as senescent, compared to other species.

Table 3 Characteristics of TreMs and habitat trees in the survey strips. “–” indicates an absence of results. “Sel”: selection cutting, “OG”: unmanaged old-growth forests

Level	Attribute	Sel1	Sel2	OG1	OG2
Stand	TreM-tree density, all species ($\text{n} \cdot \text{ha}^{-1}$)	88	48	86	68
	TreM-tree density, sugar maple ($\text{n} \cdot \text{ha}^{-1}$)	74	34	72	44
	TreM-tree density, American beech ($\text{n} \cdot \text{ha}^{-1}$)	10	14	6	18
	TreM-tree density, other species ($\text{n} \cdot \text{ha}^{-1}$)	4	0	8	6
Tree	Mean number of TreM classes per TreM-tree (n)	1.55	1.33	1.53	1.47
	TreM-tree mean DBH, all species (cm)	39.6	37.8	38.0	41.9
	TreM-tree mean DBH, sugar maple (cm)	41.2	42.1	39.4	46.1
	TreM-tree mean DBH, American beech (cm)	30.8	27.7	28.0	34.9
	TreM-tree mean DBH, other species (cm)	32.0	–	33.0	32.70
TreM	Bark loss density ($\text{n} \cdot \text{ha}^{-1}$)	42	14	46	20
	Broken branch or top density ($\text{n} \cdot \text{ha}^{-1}$)	24	2	22	12
	Crack density ($\text{n} \cdot \text{ha}^{-1}$)	4	4	2	4
	Crown deadwood density ($\text{n} \cdot \text{ha}^{-1}$)	8	8	14	20
	Saproxylic fungi density ($\text{n} \cdot \text{ha}^{-1}$)	2	2	10	4
	Trunk base rot hole density ($\text{n} \cdot \text{ha}^{-1}$)	4	4	6	2
	Trunk rot hole density ($\text{n} \cdot \text{ha}^{-1}$)	36	22	20	26
	Woodpecker lodge density ($\text{n} \cdot \text{ha}^{-1}$)	16	8	12	12

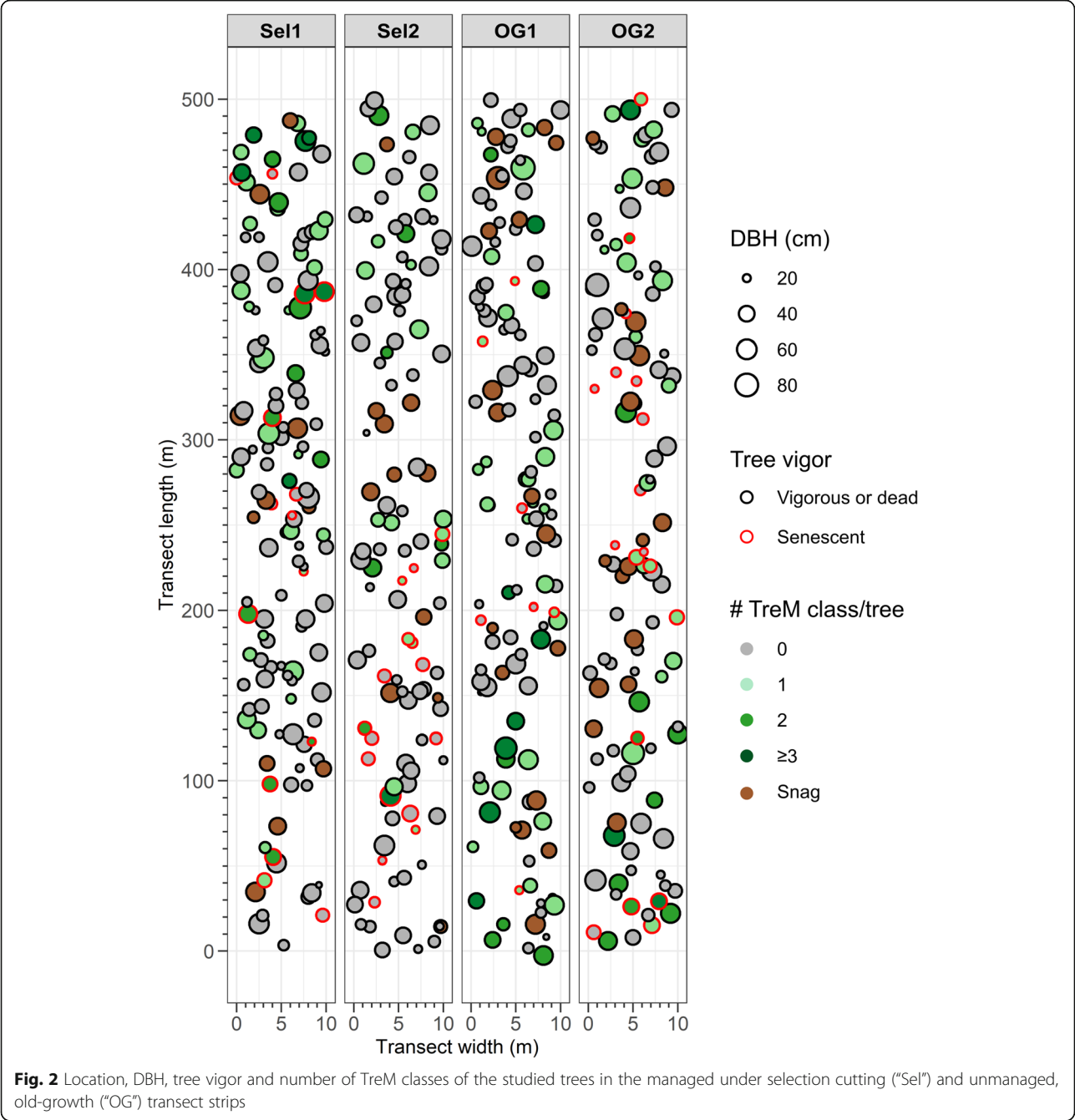
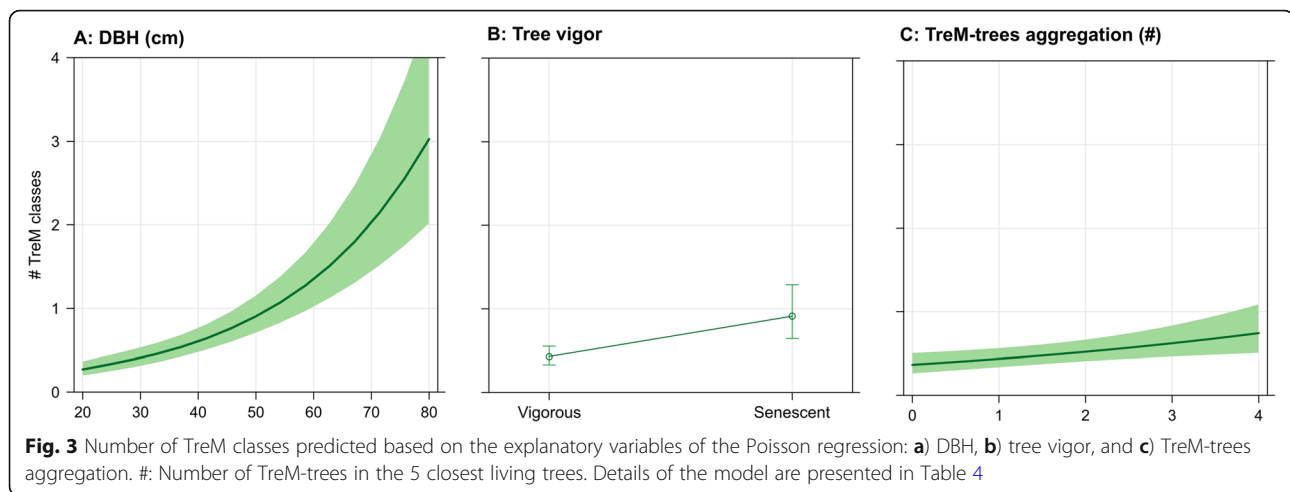


Table 4 Results of the Poisson regression analyzing the number of TreM classes per living tree. *n*: number of observations, *df*: degrees of freedom, χ^2 : chi-square, AIC: Akaike information criterion, Std.Err: standard error, ^{***}: significance at $p < 0.001$, ^{**}: significance at $p < 0.01$, ^{*}: significance at $p < 0.05$

<i>n</i>	<i>df</i>	χ^2	AIC	<i>p</i>	Variables	Estimate	Std.Err	<i>z</i> -value	Pr(< <i>z</i>)
365	4	85.64	699.12	< 0.001	Intercept	−2.503	0.254	−9.838	< 0.001 ^{***}
					DBH	0.04	0.004	9.026	< 0.001 ^{***}
					Tree vigor (senescent)	0.757	0.174	4.345	< 0.001 ^{***}
					TreM-trees aggregation	0.177	0.065	2.709	0.006 ^{**}



The DBH of sugar maple and American beech stems differed significantly and was associated with the occurrence of TreMs (Fig. 5). Sugar maples bearing at least one TreM had the largest DBH (41.7 cm), followed by sugar maples without TreMs (32.1 cm). American beeches without TreMs had the smallest DBH (25.1 cm), while those bearing at least one TreM presented intermediate values (31 cm).

For trees bearing at least 2 different TreM classes, the NMDS separated the classes into 4 groups (Fig. 6). We observed positive values on both NMDS axes for broken branches or tops as well as for woodpecker lodges, but negative values on both axes for bark loss. Trunk base rot holes, fungi and crown deadwood had negative values on the first axis of the NMDS and positive values in the second. In contrast, we observed positive values on the first axis and negative values on the second for cracks and trunk rot holes. Hence, TreM classes were recurrently grouped on a same tree according to the following associations: trunk base rot holes/fungi/crown deadwood; broken branches or tops/woodpecker lodges; crack/trunk rot holes; fungi. However, the ANOSIM underscores that forest management had no influence on these assemblages ($R = 0.024$, $p = 0.189$).

Discussion

This study provides a better understanding of the attributes at the tree- and stand-scales that drive TreM occurrence in the hardwood forests in eastern North America, where this knowledge is still scarce. It is also one of the few studies currently examining the spatial patterns of TreM-trees (Kozák et al. 2018; Puverel et al. 2019; Asbeck et al. 2020b). The occurrence of TreMs in sugar maple–American beech forests resulted both from individual tree characteristics (large DBH and low tree vigor) and, to a lower extent, from the spatial arrangement of the trees in the forest. These spatial clumps

were generally composed of several trees bearing a few TreM classes rather than by a few trees bearing several classes. Finally, we observed no marked influence of logging history on TreM-tree characteristics. Trees in un-managed stands and those in treated stands under selection cutting and former diameter-limit cuts had thus similar characteristics.

Tree size and vigor are the primary drivers of TreM occurrence in sugar maple–American beech forests

In the sugar maple–American beech forests of our study, tree DBH and vigor were the main factors influencing the probability of TreM occurrence. A higher DBH favored the presence of several TreM classes on a tree and, individually, the occurrence of all the TreM classes studied except bark loss, saproxylic fungi and trunk base rot hole. A lower tree vigor also increased the number of TreM classes on the tree and the occurrence of crown deadwood and woodpecker lodges. These positive effects of a larger DBH and of a lower tree vigor on TreMs are consistent with previous studies conducted in the coniferous or mixed forests of North America (Michel and Winter 2009; Michel et al. 2011; Martin and Raymond 2019), as well as in the mixed or hardwood forests of Europe (Larrieu and Cabanettes 2012; Courbaud et al. 2017; Paillet et al. 2019) and Middle East (Jahed et al. 2020). Indeed, a larger diameter often implies a greater age, and hence, an increased risk of biotic or abiotic damages that lead to TreM formation (Paillet et al. 2019). A larger DBH also favors the development of TreMs that are large enough to be useful for biodiversity while not threatening tree survival (Courbaud et al. 2017; Larrieu et al. 2018a). Furthermore, many TreM types are wounds that can eventually lead to tree senescence or that can be interpreted as signs of senescence (Angers et al. 2005; Martin and Raymond 2019). This implies that larger

Table 5 Results of the logistic regressions analyzing the probability of occurrence of the different TreM classes. *n*: number of observations, *df*: degrees of freedom, χ^2 : chi-square, AIC: Akaike information criterion, AUC: Area under the ROC curve, Std.Err: standard error, “***”: significance at $p < 0.001$, “**”: significance at $p < 0.01$, “*”: significance at $p < 0.05$

Model	<i>n</i>	<i>df</i>	χ^2	<i>p</i>	AIC	AUC	Variables in the final model
Bark loss	365	2	4.03	0.132	331.41	0.62	Tree vigor
Borken branch or top	365	2	38.87	< 0.001***	176.51	0.84	DBH, TreM-trees aggregation
Crack	365	2	6.00	0.049*	69.21	0.82	DBH
Crown deadwood	365	4	36.33	< 0.001***	150.70	0.83	DBH, tree vigor, management
Saproxyllic fungi	365	4	6.43	0.168	84.34	0.79	DBH, tree vigor, management
Trunk base rot hole	365	2	3.51	0.172	79.44	0.76	DBH
Trunk rot hole	365	2	25.75	< 0.001***	279.11	0.74	DBH
Woodpecker lodge	365	4	39.07	< 0.001***	147.96	0.83	DBH, tree vigor, TreM-trees aggregation

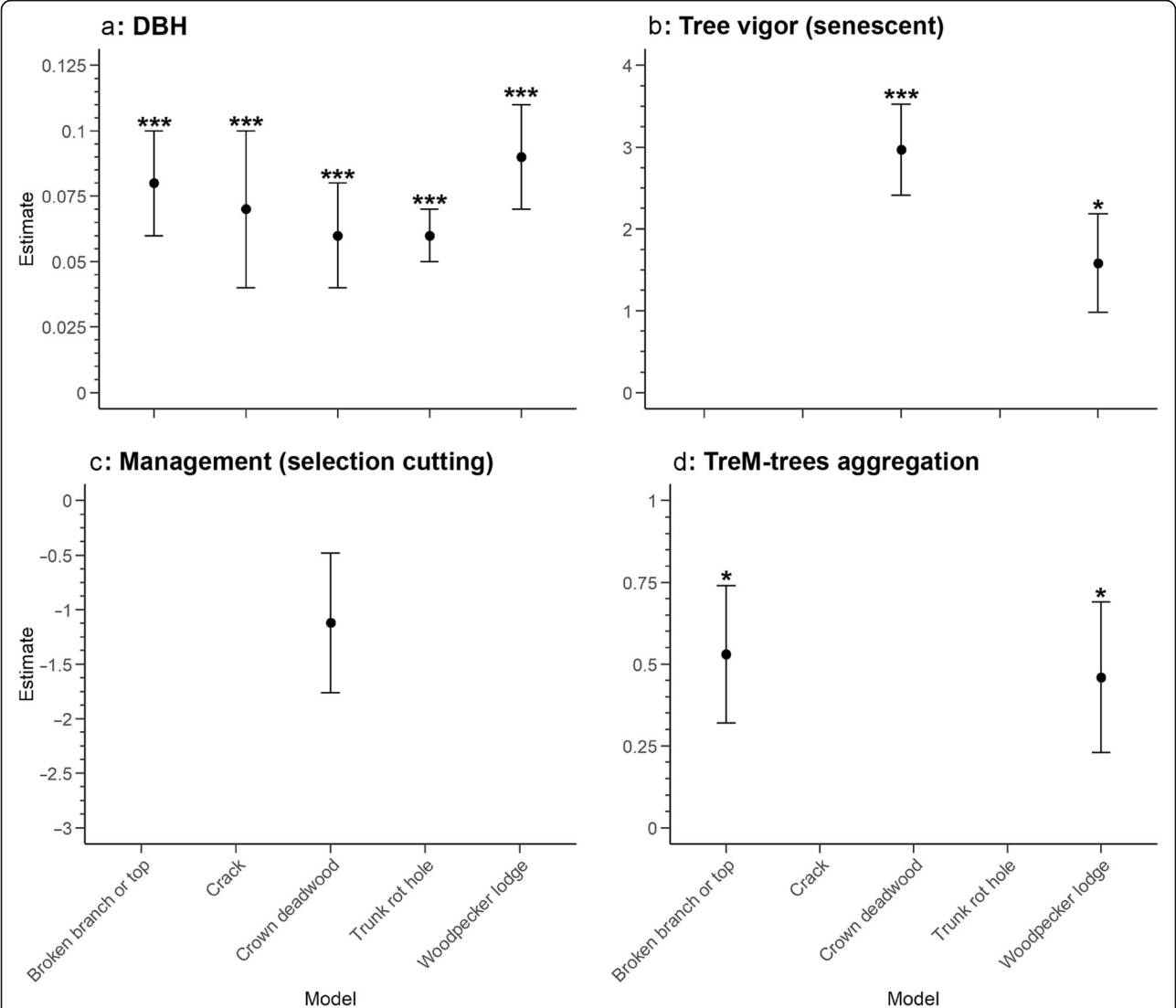


Fig. 4 Estimate, standard deviation and significance of the independent variables of the logistic regressions estimating the probability of occurrence of the different TreM classes (details of the models are presented in Table 5). No results indicate that the variable was not included in the final model. The brackets indicate for discrete variables the class to which these results apply. “***”: variable significant at $p < 0.001$, “**”: variable significant at $p < 0.01$, “*”: variable significant at $p < 0.05$. Details of the results are provided in Supplementary Table S1

Table 6 Absolute and relative frequency (in brackets) of the different TreM and tree vigor classes by species, and p -values of the pairwise comparisons for categorical data. Bold p -values indicate significant results at $p < 0.05$. ^a: Dead trees of unidentified species were not considered for the pairwise comparison of tree species within each TreM category

Category	Class	Frequency (n)				Pairwise test of independence between tree species (adjusted p -value)		
		Sugar maple (SM)	American beech (AB)	Other species (Osp)	Unknown species	SM-AB	SM-Osp	AB-Osp
TreM presence	Presence	176 (72%)	56 (23%)	12 (5%)	–	0.094	1	0.738
	Absence	172 (80%)	32 (15%)	12 (6%)	–			
TreM class	Bark loss	47 (77%)	10 (16%)	4 (7%)	–	0.003	1	0.201
	Broken branch or top	25 (83%)	2 (7%)	3 (10%)	–			
	Crack	6 (86%)	0 (0%)	1 (14%)	–			
	Crown deadwood	14 (56%)	10 (40%)	1 (4%)	–			
	Fungi	4 (44%)	5 (56%)	0 (0%)	–			
	Trunk base rot hole	8 (100%)	0 (0%)	0 (0%)	–			
	Trunk rot hole	46 (88%)	3 (6%)	3 (6%)	–			
	Woodpecker lodge	22 (92%)	2 (8%)	0 (0%)	–			
Tree vigor	Vigorous	257 (83%)	34 (11%)	18 (6%)	–	< 0.001	1	0.001
	Senescent	12 (21%)	42 (75%)	2 (4%)	–			
	Dead ^a	58 (45%)	34 (26%)	5 (4%)	32 (25%)			

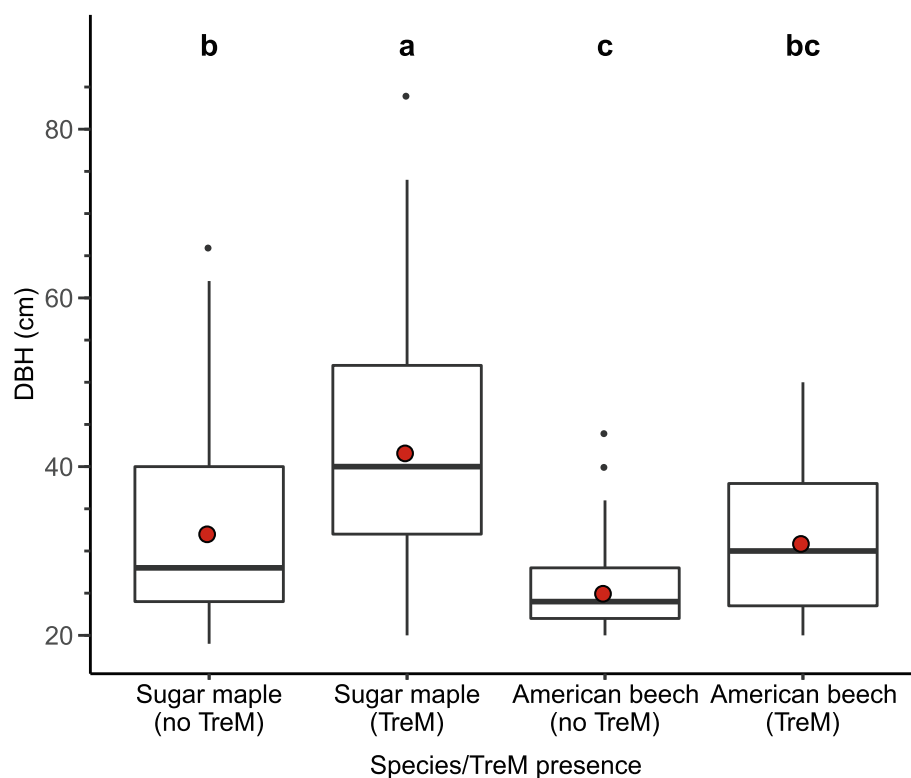
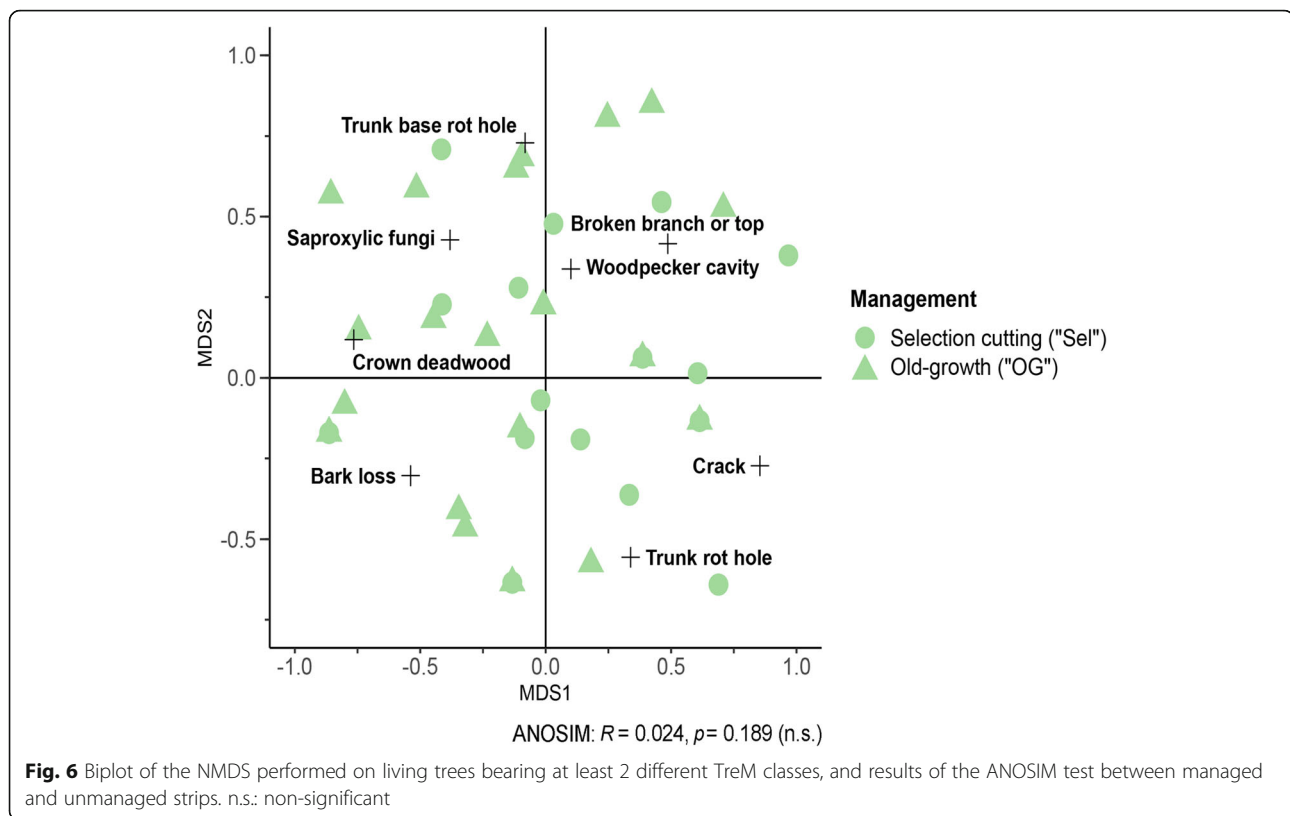


Fig. 5 Boxplot of sugar maple and American beech DBH, divided according to the occurrence of TreMs (TreM: presence of at least one TreM class; no TreM: no TreM class). Red dots indicate mean values, and letters indicate significant differences between the species/TreM classes



senescence marks are more likely to occur in old and large trees.

In this study, we also observed a weak association between TreM classes that can be considered as indicators of tree senescence (crown deadwood, fungi and trunk base rot holes; Boulet (2005)). In contrast, other TreM classes can be considered as wounds that do not necessarily threaten short-term tree survival (broken branches or tops, woodpecker lodges, cracks or trunk rot holes), although they can significantly decrease stem mechanical properties and economic value (Boulet 2005; Havreljuk et al. 2014). TreM classes indicating senescence were more often observed on American beech while wounds were more frequent on sugar maple. These results are congruent with those of Guillemette et al. (2008), who noted that sugar maples, including large individuals, are highly resistant to injuries caused by both logging operations and natural agents (e.g., bark ripped off by the fall of a neighboring tree). Beeches, on the other hand, lose vigor more easily, although the influence of BBD in this result remained unclear. The association between certain TreM classes in the studied forests is therefore probably partly species-specific.

The co-occurrence of different TreM classes observed in our transect strips was also globally consistent with previous studies, for example broken branches or top with woodpecker cavities, or cracks with rot-holes, as

well as the absence of some co-occurrences, for example between cracks and fungi (Larrieu and Cabanettes 2012; Regnery et al. 2013; Winter et al. 2015). The use of different TreM typologies between these studies however limits the comparison of the results, underlining the benefits of the homogenized typology proposed by Larrieu et al. (2018a). Overall, the factors driving TreM formation in the sugar maple–American beech forests of our study shared many common features with forests with other species compositions or in other biomes. The management of TreMs in North American forests can therefore draw on suggestions made for forests from other continents.

TreM-trees and specific TreM classes present slight spatial aggregation patterns

This is the first time, to our knowledge, that a spatial link between TreM-trees is identified. In particular, the higher the number of different TreMs classes observed, the more likely the surrounding trees were also carrying TreMs. Instead of well-delineated spatial patterns (in other words, a few trees bearing a high number TreM classes surrounded by trees without TreMs in the studied strips), we however observed a relatively slight spatial aggregation of TreM-trees. These results may be partly explained by the low number of TreM classes per tree (mean of 1.49 ± 0.76 classes per tree and a maximum of

4 classes observed on a same living tree). In uneven-aged stands, most TreM-trees indeed carry a few TreM classes, while only a few bear several TreM classes (Michel et al. 2011; Larrieu and Cabanettes 2012). As a result, the presence of TreM-trees bearing several TreM classes was generally diluted among trees bearing no TreMs or a few TreM classes in the stands. We observed a spatial aggregation only for broken branch or top and woodpecker lodge when the TreM classes were analyzed separately. The occurrence of broken branch or top often depends on relatively localized drivers (e.g., treefall or windthrow), which can explain this result. Dufour-Pelletier et al. (2020) pointed out that woodpeckers prefer to feed on spatially aggregated snags and senescent trees, even if they are relatively small in diameter. The proximity of woodpecker lodges to other TreMs trees, and thus potentially a source of food, is consistent with this behavior. It is also common for woodpeckers to forage cavities in dead branches on living trees, as the wood is softer (Martin et al. 2004; Nappi et al. 2015). The association observed between broken branch or top and woodpecker lodge can explain why the latter also presented a significant spatial pattern.

In our study, TreM-trees aggregation was never the main variable explaining the occurrence and diversity of TreMs. The relatively weak spatial links observed between TreM classes and TreM-trees can partially explain why Kozák et al. (2018) and Asbeck et al. (2020b) were unable to observe clear spatial patterns among TreM-trees in European forests. Only a selection of large trees (mean DBH > 50 cm) were however studied by Asbeck et al. (2020b), while we surveyed all trees with a DBH > 19 cm. Our methods might also be limited by the use of the TreM typology of Emberger et al. (2013). It indeed relies on 8 TreM classes, which may explain the low number of classes observed per tree. More detailed TreMs classification, such as the one defined by Larrieu et al. (2018a), where TreMs are divided in 7 forms, 15 groups and 47 types, could eventually help to better distinguish TreM spatial patterns in forest stands. Our sampling was also based on relatively narrow transects, exploring only a limited part of the immediate surroundings. Further studies, with more replications and partly based on large circular or rectangular plots (e.g., Kozák et al. 2018; Asbeck et al. 2020b) could therefore help to identify in greater detail the subtle spatial patterns highlighted in this study.

Limited impact of logging history on the characteristics of TreM-trees

Since we found no significant influence of logging history on the drivers of TreM occurrence in the studied strips, the characteristics of TreMs in the managed stand appear similar to those in the old-growth forest. We only

observed a trend for crown deadwood, with an occurrence that was negatively although not significantly influenced by management under selection cutting. The death of the canopy can indeed be considered as an indicator of impending tree death (Guillemette et al. 2008), explaining why these trees are logged in priority. It is thus possible that TreMs perceived as defects could be considered of low urgency, while defects justifying the rapid harvesting of trees were not classified as TreMs (Martin and Raymond 2019). The first symptoms of BDD (spots and then small cracks in the bark), for example, cannot be considered as TreM but may justify the urgent harvest of the tree. These results are consistent with those of Vuidot et al. (2011) in mixed French forests that were either managed or left unmanaged for 10 to more than 150 years. These authors observed no influence of forest practices on TreMs at the tree scale, but a lower diversity and density at the stand scale. This negative impact of logging practices on TreMs has long been known in Europe (Winter and Möller 2008; Larrieu et al. 2012; Regnery et al. 2013) and to a lesser extent, in eastern North America (Stevenson et al. 2006; Michel and Winter 2009). Due to the limited number of strips in our study, we cannot determine whether managed stands have a lower TreM density and diversity than natural stands in the studied territory. Many forests of eastern North America are nonetheless characterized by a smaller human impact than European forests, due to their relatively recent occidental colonization (Potapov et al. 2008; Watson et al. 2018). Over time, past diameter-limit cut practices could also have increased the proportion of poor-quality trees—most likely to bear TreMs—in managed stands (Kenefic et al. 2005; Nyland 2016). Guidelines for the protection of habitat trees have also developed in recent decades (Ontario Ministry of Natural Resources (OMNR) 2004; Ministère des Forêts de la Faune et des Parcs (MFFP) 2017), which may lead to better conservation of TreM-trees in the studied transects. Martin and Raymond (2019) hence highlighted that silvicultural practices maintaining a continuous forest cover in mixed forests presented a TreM density and diversity similar to that observed in stands characterized by a small human footprint. These authors nevertheless underscored that the cumulative impact of logging over time could lead to a loss in TreM richness similar to what is observed in Europe. As such, Stevenson et al. (2006) and Michel and Winter (2009) already observed a lower density of TreM-trees in managed forests of western North America. In the study area, the protection of habitat trees also focuses mainly on snags and little on living trees (Ministère des Forêts de la Faune et des Parcs (MFFP) 2017). For these reasons, complementary research will be necessary to better evaluate the impacts of logging practices on TreMs in the forests of North America.

Limited influence of beech bark disease on TreM formation

BBD has been reported as an important driver of tree senescence and mortality in the study area (Ministère des Forêts de la Faune et des Parcs (MFFP) 2020). It could have thus influenced TreM formation as well as spatial patterns in the strips. More than 55% of the living American beeches were classified as senescent, as opposed to less than 5% of the living sugar maples in the studied strips. Similarly, crown deadwood and fungi, two indicators of BBD, were prevalent TreM classes in American beech (Savard et al. 2005; Taylor et al. 2013). These results suggest that BBD, which probably infected the study area around 2013 (Ministère des Forêts de la Faune et des Parcs (MFFP) 2020), may have influenced TreM development on American beeches in the studied stands. In forests where this disease has been present for several decades, Kahler and Anderson (2006) identified woodpecker lodges and broken branches as common in affected beeches. These two TreM classes were rare in the American beeches we sampled, but this could be because the disease killed the larger trees first (Tubbs and Houston 1990) or, conversely, because the arrival of the disease in the study area is too recent. The threshold we used to define broken branches or tops (diameter ≥ 20 cm at the broken point) requires large trees, and woodpeckers generally favor the largest trees to excavate their cavities (Swallow et al. 1988; Remm et al. 2006; Vaillancourt et al. 2008). In our study area, beech stems were generally small: even those with TreMs had a significantly smaller DBH than sugar maples without TreMs. Beeches affected by BBD were hence most likely to present TreM classes that depend little on tree size, such as fungi and crown deadwood. It is nevertheless difficult to estimate if the trend observed will change with the progression of the disease in the forests studied. Moreover, beeches that die because of BBD generally form clumps (Senécal et al. 2018). Yet, the proportion of beeches among snags or TreM-trees (26.4% and 14.8%, respectively) was relatively close to their abundance within the living trees (22.3%). This suggests that the presence of BBD in the studied strips did not create an abnormal number of TreM-trees or large snags at that stage. The relatively recent arrival of the disease as well as the scarcity of large beeches in the strips can explain these results. Moreover, the study area is at the northern range limit of American beech (Tubbs and Houston 1990), where their growth and survival could be limited. For all these reasons, it seems unlikely that BBD markedly influenced our results.

Conclusion

TreMs are still little known in northeastern North America, and this study provides a better understanding

of the factors explaining their occurrence in temperate forests. Our results consistently link TreM characteristics in the studied forest with previous research conducted in other biomes and continents. We also both highlighted the slight spatial aggregation of TreM-trees and of specific TreM classes (broken branch and top, woodpecker lodge). Overall, TreMs were more frequent and diversified on large and/or senescent trees. Sustainable forestry practices must therefore maintain enough of these trees in managed stands to maintain viable populations of forest-dwelling species in comparison to natural forests. Such practices are coherent with those aiming to conserve old-growth forest attributes, such as deadwood or very large trees, in managed forests. Maintaining unharvested patches within managed forests to promote the development of TreMs and old-growth attributes would be congruent with the possible spatial aggregation of TreM-trees observed in this study. Moreover, the BBD had little influence on the occurrence of TreMs on living trees at the time of the survey. Harvesting infected trees to control the disease could, however, limit the supply of snags, which also provide many TreMs. It would be necessary to accurately evaluate the cost/benefit ratio of this practice, on particular on deadwood-dependant species. Finally, uncertainties remain regarding how the management history of the studied stands (an initial diameter-limit cutting followed by selection cutting) affects our results. Further research considering a greater variety of natural forests and stands with different management histories will therefore be necessary to better understand anthropogenic impacts on TreMs in North American hardwood forests. Similarly, more diverse and complete sampling designs could help to better understand the spatial patterns of TreM-trees.

Abbreviations

BBD: Beech bark disease; DBH: Diameter at breast height; OG: Unmanaged, old-growth forest; SEL: Forest under selection cutting; TreM: Tree-related microhabitat

Supplementary Information

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Additional file 1.

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Authors' contributions

MM, YB and PR defined the study and the sampling protocol. MM collected and prepared the data, performed the analyses and wrote the first draft of the manuscript. YB and PR discussed the results and commented on the

manuscript. MM wrote the final draft of the manuscript. All authors read and approved the final manuscript.

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Availability of data and materials

The datasets used and/or analyzed during the current study are available from the corresponding author on reasonable request.

Declarations

Competing interests

The authors declare no competing interests.

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