Assessing tree-related microhabitat retention according to a harvest gradient using tree-defect surveys as proxies in Eastern Canadian mixedwood forests

by Maxence Martin^{1,2,*} and Patricia Raymond^{2,3}

ABSTRACT

Tree-related microhabitats (hereafter “TreMs”) play a key role in forest biodiversity. However, harvesting may cause their erosion. In North America, knowledge about TreMs is still lacking but defect surveys are largely available in managed forests. The objectives of our study were: (1) to demonstrate that defect surveys can be a reliable resource to identify TreMs; and, (2) to evaluate the capacity of silvicultural treatments to maintain TreM abundance and diversity according to a harvest gradient. To achieve these objectives, we identified TreMs from a defect survey performed the year a harvest gradient was applied to 20 plots, including uncut control, shelterwood treatments removing 50%, 43% and 36% of basal area, and clearcut (4 plots/treatment). The density and composition of TreMs were then compared based on treatments. Overall, 38% of defects actually corresponded to TreMs, confirming that tree-defects can be used as TreM proxies. Bark loss was the most abundant TreM. While there was practically no TreM in clearcuts, all shelterwood treatments initially maintained TreM diversity and density at the same values found in uncut control plots. Shelterwood systems, especially those maintaining a continuous cover, could therefore prove helpful to sustain TreMs and their biodiversity in managed forests.

Keywords: mixedwood; wildlife habitat; forest biodiversity conservation; monitoring; tree structure; ecosystem management; disturbance-based management; multi-aged silviculture; *Femelschlag*; continuous cover; tree vigour

RÉSUMÉ

Les microhabitats des arbres (dorénavant « TreMs ») jouent un rôle clé dans la biodiversité forestière. Cependant, l'exploitation forestière peut causer leur déclin. Peu d'information est disponible sur les TreMs en Amérique du Nord, mais les inventaires de défauts sont courants. Nos objectifs étaient ainsi : 1) démontrer que les inventaires de défauts permettent d'identifier les TreMs et 2) évaluer la capacité des traitements forestiers à maintenir la diversité et la densité des TreMs selon un gradient de récolte. Nous avons identifié les TreMs à partir d'un inventaire de défauts réalisé l'année suivant l'application d'un gradient de récolte (témoin, coupes partielles retirant 50%, 43% et 36% de la surface terrière, coupe totale) dans 20 placettes (4 placettes/traitement). Nous avons ensuite comparé la densité et la composition en TreMs selon les traitements. 38% des défauts correspondaient à des TreMs, confirmant le lien entre défauts et TreMs. Le bois sans écorce était le TreM le plus abondant. Les TreMs étaient presque absents des coupes totales, mais de densité et diversité équivalentes entre le témoin et les coupes partielles. Ces types de traitements, notamment ceux conservant un couvert continu, pourraient donc aider à conserver les TreMs dans les forêts aménagées.

Mots clés: forêt mixte; habitat naturel; conservation de la biodiversité forestière; inventaire; structure des arbres; aménagement écosystémique; aménagement basé sur les perturbations; sylviculture de la futaie irrégulière; *Femelschlag*; couvert permanent; vigueur des arbres

Maxence Martin

Patricia Raymond

¹Département des sciences fondamentales, Université du Québec à Chicoutimi, 555 boul. de l'Université, Chicoutimi, Québec, G7H2B1, Canada * Corresponding author: maxence.martin1@uqac.ca

²Centre d'étude de la forêt, Université du Québec à Montréal, P.O. Box 8888, Centre-ville Station, Montréal (QC) H3C 3P8, Canada.

³Direction de la recherche forestière, Ministère des Forêts, de la Faune et des Parcs du Québec, 2700 rue Einstein, Québec, G1P 3W8, Canada

Introduction

Finding balance between conflicting economic and environmental objectives is a challenge commonly faced by forest managers (Bengston 1994; Bauhus *et al.* 2009; Puettmann *et al.* 2009). In conventional silvicultural systems, each action performed in a forest stand aims to improve its commercial quality. Therefore, trees with a high risk of dying before the next intervention or with a low economic value are first removed through thinning or selection cut (Majcen *et al.* 1990; Nyland 2002). However, by removing in priority trees that are senescent, wounded or crooked, conventional silvicultural practices have, as a downside, the removal of trees with the highest ecological value (Darveau and Desrochers 2001; Michel and Winter 2009; Dieler *et al.* 2017). As a result, management strategies focussing only on high-quality timber production can eventually lead to biodiversity issues (Puettmann *et al.* 2009; Dieler *et al.* 2017).

Tree-related microhabitats (hereafter “TreM”) are “*distinct, well delineated structure occurring on living or standing dead trees, that constitutes 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.* 2018). TreMs play a key role in forest biodiversity, along with other elements like dead wood or stand structural complexity (Darveau and Desrochers 2001; Stokland *et al.* 2012; Gao *et al.* 2015). Yet they have strongly decreased in Europe because of management strategies based on the continuous improvement of stem quality (Winter and Möller 2008; Larrieu *et al.* 2012; Dieler *et al.* 2017). Cracks, cavities or saproxylic fungi are examples of TreMs that are perceived as defects by foresters, justifying the removal of host trees for these structures (Havreljuk *et al.* 2014). The decline in TreMs is thus a relevant example of the difficulty in finding balance between stand commercial value and biodiversity conservation when managing forests with conventional silvicultural systems. Accordingly, major efforts were made in Europe over the last decades to improve the recognition and understanding of TreMs (Larrieu *et al.* 2018). As a result, active strategies for their protection were integrated into European sustainable management policies (European Commission 2015).

In North America, cavities are virtually the only TreM studied and considered in management strategies (Kenefic and Nyland 2007; Bauhus *et al.* 2009). To date, research studies about other types of TreMs have been restricted to North-western America (Michel and Winter 2009). This can be explained by the fact that cavities are particularly important for many species of birds, mammals, insects, arachnids and fungi, yet seriously threatened by forest management (DeGraaf and Shigo 1985; Ouellet-Lapointe *et al.* 2012). However, TreM-dependent species vary based on the type of TreM. For instance, species requiring cavities do not require dead branches or bark loss to thrive (Winter and Möller 2008; Larrieu *et al.* 2018). Hierarchizing TreMs is thus unsuitable, as they are complementary drivers of forest biodiversity. Overall, a better understanding of the diversity and importance of TreMs is fundamental to ensure a sustainable forest management.

Currently, the dominant forest management paradigms aim to include environmental objectives in active management strategies (Lindenmayer *et al.* 2008; Sarr and

Puettmann 2008; Dieler *et al.* 2017). In managed forests, silvicultural systems maintaining a continuous cover can preserve old-growth attributes and stand complexity and serve as promising systems to conciliate wood production and biodiversity protection (Bauhus *et al.* 2009; Raymond *et al.* 2009; Gauthier *et al.* 2018). However, even in continuous-cover systems, TreMs may progressively decline because they are recognized as defects that deplete stand quality by foresters instead of TreMs. In the absence of TreM monitoring, a TreM decline similar to that observed in Europe could occur in North American forests, especially in areas under intensive forest management.

Unlike TreM surveys, defect surveys are very common in North America because they are an essential tool for forest managers. Moreover, a significant part of the elements described in defect typology are likely to be identified as TreMs. For these reasons, defect surveys could be efficient TreM proxies in regions where this knowledge is lacking. By combining defect and TreM surveys, the most efficient silvicultural systems could actually be identified to achieve balance between stand quality improvement and biodiversity protection. Thus, the first objective of our study was to demonstrate that tree-defect surveys can be a reliable resource to identify tree-related TreMs in the absence of specific TreM surveys. We predicted that a large part of trees considered as defective in surveys are hosts to TreMs. Our second objective was to evaluate the capacity of silvicultural treatments to maintain TreM abundance and diversity according to a harvest gradient. We predicted that silvicultural treatments enabling a higher tree retention can better preserve the abundance and diversity of TreMs. To achieve these objectives, we used the experimental design described by Raymond and Bédard (2017), consisting of balsam fir (*Abies balsamea* [L.] Mill.)–yellow birch (*Betula alleghaniensis* Britton) stands under four silvicultural scenarios with a gradient of harvest intensity and where accurate defect surveys were performed.

Materials and methods

Study territory

This study used data from the irregular shelterwood experiment conducted in the Portneuf County (CPI-M1), 80 km northwest of Québec City, Canada (Raymond and Bédard 2017). This region is characterized by hilly topography with rounded tops (Robitaille and Saucier 1998). The experiment was established in balsam fir–yellow birch stands growing on thin (< 1 m) glacial upslope tills (10% slope) between 330 m and 460 m altitude. The region receives on average 1250 mm of annual precipitations, with 31% snowfall. Mean monthly temperatures (1981 to 2010) vary from -14.6 °C in January to 17.3 °C in July (using BioSIM; Regniere and Bolstad 1994). The dominant ecotype was classified as balsam fir–yellow birch with thin-to-thick deposits, medium soil texture and mesic drainage (Blouin and Berger 2003). Selected stands had irregular, uneven-aged structures (*sensu* Smith *et al.* 1997), with the oldest trees exceeding 150 years, and a majority of trees smaller than 50 cm at diameter at breast height (DBH). The presence of stumps and dendrochronological evidence of growth release indicates that partial cutting occurred during the 1960s. However, there was no evidence of previous cuts in the stands. Prior to cutting, the mean merchantable basal

area (BA) was 30 ± 3.6 m²/ha composed of 45% balsam fir, 24% red spruce (*Picea rubens* Sarg.), 16% red maple (*Acer rubrum* L.) and 12% yellow birch. The remaining BA included companion species, such as paper birch (*Betula papyrifera* Marsh.), mountain maple (*Acer spicatum* L.), pin cherry (*Prunus pensylvanica* L.f.), striped maple (*Acer pensylvanicum* L.) and American mountain-ash (*Sorbus americana* Marsh.).

Experimental design

The experiment was comprised of four complete randomized blocks, each one testing five silvicultural systems applied on 70 m × 70 m (0.49 ha) experimental units (EU). Testing was conducted from the less to the most intense harvest: (i) uncut control (0% removal, 30 m²/ha basal area); (ii) continuous cover irregular shelterwood ("CCIS", with expected 25-30 year return intervals, 19 m²/ha of residual basal area [RBA], no final cut); (iii) extended irregular shelterwood ("EIS", RBA 17 m²/ha, expected final cut after 30 years); (iv) uniform regular shelterwood ("URS", RBA 15 m²/ha, expected final cut after 10 years); and (v) clearcut with protection of regeneration and soils (harvest of merchantable trees > 9 cm DBH using spaced skid trails) (Raymond and Bédard 2017). We delimited the blocks based on location and stand composition (% merchantable BA in softwoods and hardwoods) before we randomly assigned treatments within the blocks.

Tree marking in shelterwood treatments was based on a combination of harvest priorities related to tree vigour ("MSCR" vigour classification by Boulet 2005) and species composition and diameter. We marked non-vigorous trees to be removed to improve stand quality and short-lived tree species above a specified diameter to prevent short-term mortality (balsam fir > 20 cm DBH, aspen > 24 cm and paper birch > 32 cm). Since the experiment aimed to conserve late-successional structural attributes, we also marked legacy trees to be retained in each EU: three living legacy trees > 19 cm DBH, including one veteran of long-lived tree species (i.e., red spruce or yellow birch), one yellow birch seed-tree and one cavity tree (current or potential) or fruit tree (*sensu* OMNR 2004), as recommended by current guidelines for "adapted silviculture practices" (Déry and Leblanc 2005). Standing dead trees ≥ 20 cm DBH were not cut unless they could compromise forest workers' safety (i.e., if located in the vicinity of a marked tree, within a distance equivalent to its height). Cutting was performed during the leafless period of fall 2009.

TreM identification and analysis

All merchantable trees (DBH > 9 cm) in 50 m × 50 m central study plot within each EU were numbered, mapped and characterized for species, DBH and a combined risk (i.e. vigour) and wood product class (i.e., potential sawlog or not) (Majcen *et al.* 1990) before and after the cut. We used the Boulet (2005) tree-defect typology to assess the first prediction that a large part of trees considered as defective in surveys are hosts to TreMs. The survey was performed the year following the cut. Since no defect evaluation was conducted prior to the cut, we assumed that the precut defect distribution was similar between the plots. Indeed, as the sampling design initially aimed to compare different silvicultural treat-

ments, pre-harvest stand commercial value should have been similar (i.e., the stand defects composition) among the different treatments. In addition, the plot size is relatively large in comparison to standard sizes in Québec (20 x 20 m, MFFP 2016), limiting the potential biases due to the sampling of a non-representative plot.

All defects were then identified and recorded in the study plots and their characteristics were compared with the Larrieu *et al.* (2018) typology, since their research provided the most recent and complete TreM typology at the time of this study. When the characteristics of a tree defect class matched the characteristics of a TreM, we considered that defect class as such ("TreMs"). For example, the Boulet (2005) "defect class", defined as "circular or elongated hole on the trunk with a diameter superior or equal to 10 cm" also corresponds to the Larrieu *et al.* (2018) TreM "trunk rot-hole" defined by a cavity with an opening 10 cm or over in diameter. In contrast, the defect classes that did not correspond to any TreM types were considered as "non-TreM defects." Trees without any non-TreM defects or TreMs corresponded to the "no defect" group. However, the size or number thresholds used by Boulet (2005) are often different than those suggested by Larrieu *et al.* (2018). Therefore, the thresholds were adapted to discriminate between TreMs and non-TreM defects. Nevertheless, we aimed to define biologically consistent and conservative thresholds in order to ensure the biological values of our definition of TreMs. In addition, the Boulet (2005) classification identifies for each tree the defects that most depreciates tree vigour and sawlog quality. Thus, and at the opposite of common TreMs surveys, (e.g., Winter and Möller 2008; Vuidot *et al.* 2010; Larrieu *et al.* 2012), a maximum of one defect has been recorded for each tree.

To assess the second prediction that silvicultural treatments enabling a higher tree retention better preserve the abundance and diversity of TreMs, an analysis of variance (ANOVA) was used with random effects. For each ANOVA, the treatments were used as a fixed factor and the blocks as a random factor. Firstly, an ANOVA was performed for each defect group (TreM, non-TreM defect, no defect) using density (n. trees/ha) as dependent variable. Secondly, an ANOVA was performed for each TreM class using density as the dependent variable. Finally, we performed ANOVA to compare the diversity of TreM classes among cutting treatments with the Shannon diversity index (Shannon and Weaver 1949). For all these analyses, a *post-hoc* Tukey test was performed (Kutner *et al.* 2004). When necessary, we performed data transformation (square-root, log2 or outlier removal) to meet ANOVA requirements. An ANOVA was not carried out for TreM classes that had fewer than 20 observations in all plots combined (i.e., bark shelter, fork split, epicormic shoots, sap run and heavy resinosis, and burr).

Statistical analyses were completed using R-software, version 3.3.1 (R Core Team 2016) with the nlme (Pinheiro *et al.* 2016), emmeans (Russel 2018) and ggplot2 (Wickham 2016) packages based on $\alpha = 0.05$.

Results

TreM identification

Among the defects inventoried in the survey (Appendix S1), 13 TreM classes and 10 non-TreM defect classes were identi-

Table 1. Classification of defects by type, TreM category and class, and related thresholds according to Boulet *et al.* (2004) and Larrieu *et al.* (2018) typologies. Note that Larrieu *et al.* (2018) did not propose any thresholds for non-TreM defects. *Potential TreM users were defined according to the Larrieu *et al.* (2018) literature review.

Defect group	Category	Class	Code	Boulet (2005)	Larrieu <i>et al.</i> (2018)	Comments	Potential users*
TreM	Cavity	Trunk cavity or rot-hole	TCR	Any origin, $\varnothing > 10$ cm	All $\varnothing$ if woodpecker-origin; $\varnothing > 10$ cm in other cases	No indication of cavity origin in the defect	Mammals, birds, amphibians, insects, arachnids, typology bryophytes, fungi, lichens
		Trunk base rot-hole	TBR	Cavity or scar on the trunk stump; no threshold	Ground contact, $\varnothing > 10$ cm	Partially rotten scars and un-rotten scars grouped under the same defect classes in the typology	Mammals, birds, amphibians, insects, arachnids, bryophytes, fungi, lichens
	Trunk	Canker	CAN	Rot depth ≥ 5 cm; main depreciating defect	Largest $\varnothing > 20$ cm or large part of the trunk covered	No indication of canker surface in defect typology, rot depth as unique available threshold	Insects, bryophytes, fungi
		Bark shelter	BAS	Covering at least one face of the trunk; main depreciating defect	Gap > 1 cm; depth > 10 cm; height > 10 cm	Parameters used by Larrieu <i>et al.</i> (2018) absent in Boulet (2005)	Mammals, birds, gastropods, insects, fungi
		Bark loss	BAL	Trunk wounded to the sapwood; main depreciating defect	300 cm ² (A5 format) of sapwood exposed	Parameters used by Larrieu <i>et al.</i> (2018) absent in Boulet (2005)	Mammals, birds, gastropods, insects, fungi
		Large crack	CRA	[Length > 1.5 m] or [length ≤ 1.5 m, largest width ≥ 10 cm, depth ≥ 5 cm]	Length > 30 cm; width > 1 cm; depth > 10 cm	Length > 1.5 m considered as conservative enough in comparison with Larrieu <i>et al.</i> (2018) thresholds	Mammals, birds, gastropods, insects, arachnids, fungi, lichens
		Fork split	FOS	Not healed, close to breakage	Length > 30 cm	Parameters used by Larrieu <i>et al.</i> (2018) absent in Boulet (2005)	Mammals, birds, gastropods, insects, arachnids, fungi, lichens
	Top	Dead or broken branch	DBB	$\varnothing > 20$ cm	$\varnothing > 10$ cm	Different diameter thresholds between the typologies	Birds, insects, arachnids, fungi, lichens
		Dead top	DET	$> 25\%$ of the crown is dead	Branch $\varnothing > 3$ cm and $> 10\%$ of the crown is dead	Different thresholds and indicators between the typologies	Birds, insects, arachnids, fungi, lichens
	Small	Epicormic shoots	EPS	Main depreciating defect	> 5 twig clusters	Parameters used by Larrieu <i>et al.</i> (2018) absent in Boulet (2005)	Birds, arachnids
		Burr	BUR	Main depreciating defect	Largest $\varnothing > 20$ cm	Parameters used by Larrieu <i>et al.</i> (2018) absent in Boulet (2005)	Insects, bryophytes, fungi
		Fungi	FUN	Any fungi causing wood decay	Various according to the fungus species	Different fungus species between Europe and North America	Gastropods, insects, arachnids, bryophytes, fungi

Defect group	Category	Class	Code	Boulet (2005)	Larrieu <i>et al.</i> (2018)	Comments	Potential users*
Non-TreM Defect		Healed wound	HEW	Scar of an ancient wound	–	–	–
		Superficial bark wound	BAW	Trunk wounded on the bark only	–	–	–
		Minor top mortality	LTM	≤25% of the crown is dead	–	–	–
		Small cavity	SMC	ø≤10 cm	–	–	–
		Shape defect	SHD	Defect influencing only tree shape	–	–	–
		Small crack	SCR	Length ≤1.5 m and largest width <10 cm or depth <5 cm	–	–	–
		Clump shoot	CLS	–	–	–	–
		Small canker	SCA	Cover less than one face of the trunk	–	–	–
		Wounded or rotten root	WRR	Root broken or rotten	–	–	–
		Insect holes	INH	Opening of insect gallery on the trunk	–	–	–
No Defect		No defect	NOD	–	–	No defect or TreM identified for the tree	–

fied (Table 1). Tree TreM classes can be grouped in four overarching categories: cavity, trunk, top and small TreMs. Defects corresponding to TreMs were observed in 26% of the sampled trees (873 trees). Trees with non-TreM defects made up the most abundant group, 43% of the sampled trees (1435 trees), followed by trees without any defects, 31%, (1049 trees). Thus, a great portion of the trees defined by the presence of at least one defect are actually hosts to TreMs (38%), implying a significant importance for stand biodiversity. Tree-bearing TreMs were more abundant for broadleaved species than for coniferous, while it was the opposite for non-TreM defects and no defect trees (Appendix S2). The DBH of trees hosts to TreMs varied strongly depending on tree species and TreM class (Appendix S3).

The most abundant TreM class was bark loss (mean density: 43 trees/ha), while the least abundant were epicormic shoots and fork splits (0.2 trees/ha and 0.1 trees/ha, respectively). Other TreM mean densities ranged from 14 trees/ha (dead top) to 0.4 trees/ha (bark shelter). For non-TreM defects, the most abundant class was bark wound (56 trees/ha), and the less abundant class was clump shoots (4 trees/ha). Thus, there was a strong variation among classes for both TreMs and non-TreM defects. In addition, most of the superficial bark wound (83%) corresponded to cracks on balsam fir bark, indicative of root rot.

Effects of silvicultural treatments on TreM tree density

Tree density differed among treatments for all defect groups: TreMs ($p<0.001$), non-TreM defects ($p<0.001$) and no defect ($p<0.001$). Overall, each defect group was more abundant in

the control than in the clearcut treatment, while they did not differ among the three shelterwood treatments (Fig. 1). Shelterwood treatments maintained a mean TreM density equivalent to that observed in the control (e.g., 124 trees/ha in control, from 85 to 106 trees/ha in shelterwood treatments and 27 trees/ha in the clearcut). In contrast, shelterwood treatments decreased the density of trees showing non-TreM defects and defect-free trees, but the reduction was much less important than with the clearcut (e.g., 310 defect non-TreM trees/ha and 211 no-defect trees/ha in control, from 119 to 156 defect non-TreM trees/ha and 85 to 117 no-defect trees/ha in shelterwood treatments, 11 defect non-TreM trees/ha and 23 no-defect trees/ha in the clearcut). The only exception was for the no defect free trees in extended regular shelterwood treatments, with a density similar to that observed in the clearcut.

Effects of silvicultural treatments on TreM diversity and composition

Comparison among the treatments using the Shannon index showed that shelterwood treatments had a diversity of TreMs equivalent to the control and, on average, three times greater than in the clearcut ($p<0.05$; Fig. 2). Overall, we found differences in density among treatments for five TreM classes: trunk cavity or rot-hole, bark loss, large crack, dead or broken branches and dead top (Table 2). Dead tops and large cracks were more abundant in the control treatment than in any other treatments (respectively $p<0.001$ and $p<0.05$; Fig. 3). Dead top density was also higher in uniform regular shelterwood than in irregular shelterwood treatments and the

Fig. 1 Boxplots of tree density by treatment for **(A)** TreMs, **(B)** non-TreM defects and **(C)** no defect. Letters represent significantly different values and diamonds mean values. CTRL: control; CCIS: continuous irregular shelterwood cutting (RBA: 19 m²/ha); EIS: extended irregular shelterwood cutting (RBA: 17 m²/ha); URS: uniform regular shelterwood cutting (RBA: 15 m²/ha); CCT: clearcut

clearcut. Extended irregular shelterwood was the only treatment with the same density of large cracks as the clearcut. Trunk cavity or rot-hole was more abundant in the control than in the clearcut ($p < 0.05$). Bark loss was greater in the three shelterwood treatments than in the clearcut, but not greater than in the control ($p < 0.05$). Dead and broken branches were in higher density in the continuous irregular shelterwood than in the clearcut ($p < 0.05$). Finally, there was no significant variation in the density of trunk-base rot-hole, canker and fungi TreMs. The mean density of tree bearing fungi was higher in the control in comparison to the other treatments, but this result was mostly due to two outliers in control plots. When the outliers influence was smoothed through data transformation, there was no difference among treatments.

Discussion

The assessment of tree-related TreMs using the Boulet (2005) defect survey method showed a significant correspondence between the defect classes and TreMs. The study revealed that numerous defect trees were actually TreM hosts and may have an important biological value for the stands. We also found that the overall density of TreM-host trees and their diversity in shelterwood treatments were similar to those measured in the control, regardless of the harvest intensity. However, the small shifts observed in TreM composition indicate that some TreM classes like large cracks could be replaced by others like bark loss over time in managed stands.

Tree-defects as relevant TreM proxies

To our knowledge, this is the first time that TreMs and tree defects are directly linked. The results hence support the evidence of a relationship that has often been evoked in the past. Previous studies hypothesized that the perception of TreMs as defects by forest managers caused their erosion in managed stands (Winter and Möller 2008; Michel and Winter 2009; Regnery *et al.* 2013). Similarly, Havreljuk *et al.* (2014) proposed to maintain defect-bearing trees to meet biodiversity goals in management planning. This implies an acknowledgement of the contribution of defective trees to forest biodiversity. However, achieving biodiversity conservation objectives requires the integration of TreM objectives in current management practices (Dieler *et al.* 2017). For this reason, the link between TreMs and defects needs to be clarified and acknowledged by both forest managers and ecologists because defects and TreMs are often the two sides of the same coin.

Overall, the thresholds used for our typology based on Boulet (2005) were rarely similar to those suggested by Larrieu *et al.* (2018). However, they were often more conservative. The most striking example is the “trunk-base rot-hole” class

for which the corresponding Boulet (2005) defect classes are divided throughout a 60 cm-diameter threshold, much larger than the 10 cm-diameter suggested by Larrieu *et al.* (2018). Because of this large gap between the two thresholds, we retained no size threshold for this TreM. Thus, no additional restriction was added for this class and all trunk-base rot-hole defects using Boulet (2005) were considered as TreMs. Similarly, the Boulet (2005) thresholds are more conservative than the Larrieu *et al.* (2018) thresholds for woodpecker breeding cavities, dead or broken branches and dead tops. This implies that some defects non-retained as TreM in this study still could have a significant importance for biodiversity. Furthermore, specific size or number thresholds were sometimes absent in the Boulet (2005) defect classes, especially for burrs, sap runs/heavy resinosis, fungi and epicormics shoots. However, it was assumed that if such defect classes were considered as the main depreciating ones, it was likely to achieve the Larrieu *et al.* (2018) thresholds. The Larrieu *et al.* (2018) typology was also defined for European temperate forests and it was also possible that some of these thresholds are not relevant in northeastern American forests. Finally, not all TreMs are defects, such as bird nests or epiphytic plants (Vuidot *et al.* 2010; Michel *et al.* 2011; Larrieu *et al.* 2018). Therefore, it is likely that non-defects TreMs have not been identified in the stands in this study. Nevertheless, we found that many trees that could be classified as defective by Boulet (2005) shared similar TreM characteristics described by Larrieu *et al.* (2018), implying that such a typology of tree defects could be used as a proxy for TreM surveys.

The density variation in TreM class is consistent with studies in European broadleaved or mixedwood forests. For example, TreM classes identified by Möller *et al.* (2008) ranged from 0.5 to 62 TreMs/ha, while those identified by Larrieu *et al.* (2012) ranged from 1 to 35 TreMs/ha. However, the defect survey method of Boulet (2005) used in this study only considered one defect or TreM for each tree, i.e., the most depreciating one, while tree hosts of more than one TreM are common, especially for the largest ones (Vuidot *et al.* 2010; Larrieu *et al.* 2014). It is therefore likely that TreM density in the stands in this study is superior to the density of TreM host trees. In addition, the Boulet (2005) methodology only survived live trees, while dead trees are an important TreM resource (Vuidot *et al.* 2010; Larrieu *et al.* 2012; Siitonen 2012). Standing dead trees that presented no risk for workers were maintained in each treatment and were still abundant in the study plots (Martin 2014). This implies that snags were an important contributor to TreM richness and diversity.

Potential of silvicultural systems using partial cuts to maintain TreMs in managed forests

By removing almost all the merchantable trees, clearcutting cause a significant decrease in TreM abundance. They also strongly limit their recruitment in future decades. TreM density increases with stand age or individual tree size, and often

Fig. 2 Boxplot of Shannon index values by TreM classes and cutting treatments. Letters represent significantly different values and diamonds, mean values. CTRL: control; CCIS: continuous irregular shelterwood cutting (RBA: 19 m²/ha); EIS: extended irregular shelterwood cutting (RBA: 17 m²/ha); URS: uniform regular shelterwood cutting (RBA: 15 m²/ha); CCT: clearcut")

requires minimum tree size to appear or to fulfill their ecological roles (Michel *et al.* 2011; Regnery *et al.* 2013; Larrieu *et al.* 2014). For example, woodpeckers mainly excavate cavities in trees with a DBH $\geq$ 20 cm (Holloway *et al.* 2007; Vailancourt *et al.* 2008). Consequently, the TreM density and quality in clearcut stands will remain low over decades, as they are mostly constituted of young and small trees (Larrieu *et al.* 2017). Moreover, in clearcutting systems, stands are often harvested at a relatively young age compared with natural stand dynamics (Bergeron *et al.* 2002). This implies that TreM density, recruitment and functionality are restricted in these stands, as trees are cut before they reach an age or a size favourable to TreM development. Hence, clearcutting is the least suitable forest treatment for a sustainable and efficient TreM management.

In contrast, shelterwood systems have a good potential to maintain TreM density and diversity similar to those observed in unmanaged stands. Despite a rather narrow range of residual basal areas tested in the shelterwood treatments, each of these treatments had a specific impact on post-harvest stands structure and regeneration (Raymond and Bédard 2017). Thus, the similarity in TreM abundance and diversity between the shelterwood treatments seemingly mainly results from the prior harvest of non-TreM defects bearing trees. However, in the very long-term, the cumulative effect of successive harvests and thinnings can decrease TreM abundance and diversity, as observed in Europe (Larrieu *et al.* 2018). The high TreM abundance observed in this study may be explained by the more recent management history in

Table 2. Summary of treatment effects on tree density and Shannon index values by defect group and TreM class. A dash indicates that no analysis was performed for a given TreM because of low abundance (i.e., less than 20 records)

Defect Group	Category	Class	Analysis		
			Dependent Variable	Transformation	ANOVA <i>p</i> -value
TreM	All	All	Density	No transformation	<0.001
Non-TreM defect	All	All	Density	No transformation	<0.001
No defect	All	All	Density	No transformation	<0.001
TreM	Cavity	Trunk cavity or rot-hole	Density	No transformation	<0.05
		Trunk base rot-hole	Density	Square root	n.s.
	Trunk	Canker	Density	Square root	n.s.
		Bark shelter	-	-	-
		Bark loss	Density	Square root	<0.05
		Large crack	Density	-	<0.05
		Fork split	-	-	-
	Top	Dead or broken branch	Density	No transformation	<0.05
		Dead top	Density	Outlier removal (2 units)	<0.001
	Small	Epicormic shoots	-	-	-
		Sap run/heavy resinosis	-	-	-
		Burr	-	-	-
		Fungi	Density	Log2	n.s.
	All	All	Shannon index	No transformation	<0.05

North American forests. Furthermore, future entries will also greatly influence stand structural characteristics. In the continuous irregular shelterwood system, stand structure is expected to remain complex with the constant presence of trees of various sizes. However, uniform and extended shelterwood systems will have their overstory harvested once the regeneration is established (e.g., at 10 and 30 years), leading to either even-aged or two-aged stand structures. Therefore, even if these shelterwood systems provide better TreM conservation than clearcuts in the short-term, their medium-term effects will be similar. By maintaining old and mature trees, the continuous irregular shelterwood system is the one with the best potential for sustainable TreM management (Bauhus *et al.* 2009; Raymond *et al.* 2009). Nevertheless, silvicultural systems likely to maintain a continuous forest cover can eventually cause a decrease in large trees or TreM densities in the absence of specific retention conditions for old-growth forest attributes (Dieler *et al.* 2017). However, TreM recruitment is also a dynamic process (Regnery *et al.* 2013), and densities found in harvested stands can continue to change in the future. The results of our study only provide a picture of the stands immediately after harvesting; but it is likely that TreMs will differ at the time of the next entry. For these reasons, long-term monitoring of the cumulative effects of partial cuts in North American forests will be necessary to ensure that they do not result in TreM depletion.

Because large cracks are the most depreciating defect for log quality along with fungi, this TreM was the one that decreased the most after shelterwood cutting (54% to 74% less abundant than the control) (Havreljuk *et al.* 2014). Still,

with approximately 5.6 trees/ha, the density of trees with large cracks in the stands under shelterwood cuts was close to the density observed in European or northwestern American forests, ranging from 4 to 13 trees/ha in the reference stands (Winter and Möller 2008; Michel and Winter 2009; Larrieu *et al.* 2012). Species using this TreM, such as bats (Larrieu *et al.* 2018), should not be affected by the decrease; however, further study would be necessary to assess this observation. Conversely, the density of trees with bark loss slightly increased in shelterwood treatments. This TreM is often more abundant in managed than in unmanaged forests (Winter and Möller 2008; Vuidot *et al.* 2010; Larrieu *et al.* 2012), probably because they may result from logging wounds. Similarly, some treatments favoured particular TreM classes, such as dead top in the uniform regular shelterwood cutting system and dead or broken branches in the continuous shelterwood cutting systems. The high level of harvest intensity (50% removal) in the regular shelterwood may have increased sensitivity to wind damage and reduced space for operating the cuts and the less intense continuous cover irregular shelterwood (36% removal) may have contributed to increase damage to residual trees. The absence of pre-harvest TreM inventory is a limit in our study. Further research is needed to highlight how shelterwood treatments may influence the development of specific TreMs caused by harvest wounds or by post-harvest changes in the stand structure.

The similarity of the Shannon diversity index between the control and the shelterwood treatments could be explained by the slight increase in wounded or senescent trees in the

Fig. 3 Boxplot of Shannon index values by TreM classes and cutting treatments. Letters represent significantly different values and diamonds, mean values. CTRL: control; CCIS: continuous irregular shelterwood cutting (RBA: 19 m²/ha); EIS: extended irregular shelterwood cutting (RBA: 17 m²/ha); URS: uniform regular shelterwood cutting (RBA: 15 m²/ha); CCT: clearcut

harvested stands likely to compensate for the removal of trees with large cracks. These changes are moderate but can indicate a potential shift in TreM composition likely to increase with repetitive harvests. Even moderate changes in TreM diversity can have a significant impact on specialized species, which depends on specific TreMs (e.g., Gossner *et al.* 2016). TreMs associated to a greater decrease in sawlog value may particularly be impacted, to the benefit of TreMs less likely to

affect sawlog value. Yet an increase in the density of wounded or senescent trees may counterbalance overall TreM recruitment. Thus, it is hard to determine how the assemblage of TreM types will evolve over the next years. This also highlights the importance of monitoring TreMs on a regular basis in managed stands. When planning cuts in shelterwood systems, defect surveys are performed to ensure that the successive cuts will not cause stand quality depletion. These surveys

would be also a good opportunity to identify TreMs. Developing a methodology combining defect and TreM surveys could therefore be an efficient solution to monitor changes in TreM abundance and composition over time.

Conclusion

As predicted, a significant proportion (38%) of tree defects actually correspond to TreMs because TreMs and defects are often the two faces of the same coin. Accordingly, the biological value of these defects should be acknowledged in sustainable forest management. However, knowledge about TreMs in North American forests is still lacking. Defect surveys could be used as proxies of TreM surveys to facilitate operational assessment in forest management. Yet TreMs are already an indirect approach to monitor biodiversity (Paillet *et al.* 2018). Using defects as TreM proxies should be then a temporary solution as they are less precise than TreM surveys. The Boulet (2005) methodology could be therefore modified to better integrate TreMs in defect surveys, for example, by 1) monitoring all the TreMs present on trees, 2) including dead wood in the surveys, 3) considering non-defect TreMs, and 4) adapting the TreMs and their thresholds to the northeastern American context, as Larrieu *et al.* (2018) is a typology for European temperate forests.

Silvicultural systems enabling the maintenance of a continuous forest cover, such as irregular shelterwood, are the most promising for efficient TreM conservation. One third of the main depreciating defects corresponded to TreMs, implying that improving stand quality could be relatively easy to conciliate with biodiversity protection by focusing the harvests on tree-bearing non-TreM defects. Conversely, clearcut systems cause the most important declines in TreMs, and stand rejuvenation strongly limits their recruitment in future decades. However, biodiversity loss associated with each type of TreM in northeastern American mixedwood forests is still relatively unknown. Performing similar TreM research studies in undisturbed stands — an option more achievable in North America than Europe — would be helpful to better understand how to integrate TreMs in managed forests.

As a conclusion, future work on northeastern American TreMs could focus on: (1) constructing a TreM typology relevant to northeastern America, based on pre-existing European and northwestern American typologies; (2) assessing the biodiversity related to each TreM types in northeastern America; and, (3) creating typologies combining defects and TreM surveys to ensure their sustainable management.

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Appendix S1. Correspondence between the Boulet (2005) defect typology and the TreM typology used in this study for each defect class and number of trees sampled for each defect

Boulet (2005) Code	Type	Group	Class	N sampled	Boulet (2005) Code	Type	Group	Class	N sampled
DB01X	Non-TreM defect	–	Shape defect	19	DB36X	TreM	Trunk	Bark loss	2
DB02A	TreM	Top	Dead or broken branch	6	DB38A	TreM	Small	Burr	1
DB02X	TreM	Top	Dead or broken branch	3	DB38X	TreM	Small	Burr	2
DB03X	Non-TreM defect	–	Clump shoot	2	DB40E	Non-TreM defect	–	Shape defect	272
DB04X	Non-TreM defect	–	Bark wound	37	DB40X	Non-TreM defect	–	Shape defect	62
DB05A	TreM	Trunk	Bark loss	22	DB41X	Non-TreM defect	–	Shape defect	5
DB05X	TreM	Trunk	Bark loss	48	DB42X	TreM	Top	Dead or broken branch	2
DB06A	TreM	Trunk	Bark loss	67	DB43X	Non-TreM defect	–	Shape defect	5
DB06E	TreM	Trunk	Bark loss	2	EN01X	Non-TreM defect	–	Small cavity	46
DB06X	TreM	Trunk	Bark loss	17	EN02E	TreM	Cavity	Trunk cavity or rot-hole	26
DB07A	TreM	Trunk	Bark loss	18	EN02X	TreM	Cavity	Trunk cavity or rot-hole	5
DB07X	TreM	Trunk	Bark loss	53	EN03X	TreM	Cavity	Trunk cavity or rot-hole	4
DB08X	TreM	Small	Epicormic shoots	1	EN04A	TreM	Cavity	Trunk cavity or rot-hole	26
DB09A	Non-TreM defect	–	Shape Defect	2	EN04X	TreM	Cavity	Trunk cavity or rot-hole	3
DB09E	Non-TreM defect	–	Shape defect	5	EN05E	Non-TreM defect	–	Small cavity	1
DB09X	Non-TreM defect	–	Shape defect	21	EN05X	Non-TreM defect	–	Small cavity	1
DB10X	Non-TreM defect	–	Shape defect	41	EN07X	Non-TreM defect	–	Small cavity	6
DB11X	Non-TreM defect	–	Low top mortality	7	EN08X	Non-TreM defect	–	Small cavity	3
DB12X	Non-TreM defect	–	Shape defect	4	EN30X	Non-TreM defect	–	Small cavity	2
DB13X	TreM	Small	Burr	1	EN31X	Non-TreM defect	–	Small cavity	2
DB14A	TreM	Small	Burr	2	EN32E	TreM	Top	Dead or broken branch	1
DB14X	TreM	Small	Burr	2	EN33A	Non-TreM defect	–	Small cavity	1
DB17X	Non-TreM defect	–	Shape defect	1	EN33X	Non-TreM defect	–	Small cavity	3
DB18A	Non-TreM defect	–	Shape Defect	2	FE01X	Non-TreM defect	–	Shape defect	2
DB18X	Non-TreM defect	–	Shape Defect	2	FE02A	TreM	Trunk	Large crack	3
DB19X	Non-TreM defect	–	Shape defect	4	E02E	TreM	Trunk	Large crack	9
DB20A	TreM	Trunk	Bark loss	1	FE02X	Non-TreM defect	–	Small crack	32
DB20E	TreM	Trunk	Bark loss	6	FE03X	Non-TreM defect	–	Small crack	3
DB20X	TreM	Trunk	Bark loss	1	FE04A	Non-TreM defect	–	Healed wound	11
DB21A	TreM	Trunk	Bark loss	1	FE04X	Non-TreM defect	–	Healed wound	19
DB21E	TreM	Trunk	Bark loss	2	FE06A	TreM	Trunk	Large crack	27
DB21X	TreM	Trunk	Bark loss	1	FE06E	TreM	Trunk	Large crack	8
DB30E	Non-TreM defect	–	Shape defect	25	FE06X	TreM	Trunk	Large crack	4
DB30X	Non-TreM defect	–	Shape defect	3	FE07X	Non-TreM defect	–	Healed wound	2
DB31X	Non-TreM defect	–	Clump shoot	5	FE08A	Non-TreM defect	–	Healed wound	1
DB32X	TreM	Top	Dead or broken branch	3	FE08X	Non-TreM defect	–	Healed wound	1
DB33E	TreM	Top	Dead top	2	FE09X	TreM	Trunk	Large crack	5
DB33X	TreM	Top	Dead top	62	FE10X	TreM	Trunk	Large crack	2
DB34E	TreM	Top	Dead top	4	FE11X	TreM	Trunk	Large crack	2
DB34X	TreM	Top	Dead top	22	FE12X	TreM	Trunk	Large crack	1
DB35A	TreM	Trunk	Bark loss	8	FE13E	Non-TreM defect	–	Healed wound	2
DB35E	TreM	Trunk	Bark loss	115					
DB35X	TreM	Trunk	Bark loss	60					
DB36A	TreM	Trunk	Bark loss	1					

Boulet (2005) Code	Type	Group	Class	N sampled	Boulet (2005) Code	Type	Group	Class	N sampled
FE13X	Non-TreM defect	–	Healed wound	1	NC07X	Non-TreM defect	–	Small canker	23
FE15X	Non-TreM defect	–	Bark wound	1	NC11X	TreM	Trunk	Bark shelter	3
FE16A	Non-TreM defect	–	Clump shoot	2	NC30XC	TreM	Trunk	Canker	19
FE16E	Non-TreM defect	–	Clump shoot	4	NC32E	TreM	Trunk	Bark shelter	1
FE16X	Non-TreM defect	–	Clump shoot	2	NC33X	Non-TreM defect	–	Bark wound	2
FE30E	Non-TreM defect	–	Small crack	1	PR01E	TreM	Cavity	Trunk base rot-hole	7
FE30X	Non-TreM defect	–	Small crack	17	PR01X	TreM	Cavity	Trunk base rot-hole	7
FE31A	Non-TreM defect	–	Small crack	5	PR02E	Non-TreM defect	–	Healed wound	2
FE31X	Non-TreM defect	–	Small crack	11	PR02X	Non-TreM defect	–	Healed wound	1
FE33X	TreM	Trunk	Large crack	4	PR03A	TreM	Cavity	Trunk base rot-hole	7
FE34X	Non-TreM defect	–	Small crack	1	PR03E	TreM	Cavity	Trunk base rot-hole	4
FE35E	TreM	Trunk	Large crack	453	PR03X	TreM	Cavity	Trunk base rot-hole	1
FE35X	TreM	Trunk	Large crack	1	PR04E	Non-TreM defect	–	Healed wound	1
FE36A	TreM	Trunk	Fork split	2	PR04X	Non-TreM defect	–	Healed wound	2
FE36E	Non-TreM defect	–	Healed wound	1	PR05X	Non-TreM defect	–	Healed wound	5
FE36X	Non-TreM defect	–	Healed wound	2	PR07A	Non-TreM defect	–	Wounded or rotten root	4
HP01A	Non-TreM defect	–	Low top mortality	14	PR07E	Non-TreM defect	–	Wounded or rotten root	5
HP01E	Non-TreM defect	–	Low top mortality	2	PR07X	Non-TreM defect	–	Wounded or rotten root	4
HP01X	Non-TreM defect	–	Low top mortality	5	PR30E	TreM	Cavity	Trunk base rot-hole	3
HP02A	TreM	Top	Dead top	1	PR31A	TreM	Cavity	Trunk base rot-hole	3
HP02E	TreM	Top	Dead top	8	PR31X	TreM	Cavity	Trunk base rot-hole	9
HP02S	TreM	Top	Dead top	4	PR32A	Non-TreM defect	–	Wounded or rotten root	4
HP02X	TreM	Top	Dead top	2	PR32E	Non-TreM defect	–	Wounded or rotten root	6
HP03E	TreM	Top	Dead top	2	PR32X	Non-TreM defect	–	Wounded or rotten root	8
HP03X	TreM	Top	Dead top	1	SP06X	TreM	Small	Fungi	3
HP04X	TreM	Top	Dead top	4	SP09A	TreM	Small	Fungi	1
HP06A	TreM	Top	Dead top	7	SP10A	TreM	Small	Fungi	3
HP06E	TreM	Top	Dead top	1	SP10X	TreM	Small	Fungi	1
HP07X	TreM	Top	Dead top	13	SP12S	TreM	Small	Fungi	1
HP11A	TreM	Top	Dead or broken branch	2	SP12X	TreM	Small	Fungi	1
HP11E	TreM	Top	Dead or broken branch	7	SP14A	TreM	Small	Fungi	16
HP11X	TreM	Top	Dead or broken branch	3	SP15X	TreM	Small	Fungi	1
HP12X	Non-TreM defect	–	Shape defect	3	SP16X	TreM	Small	Fungi	17
HP33A	Non-TreM defect	–	Low top mortality	1	SP34X	TreM	Small	Fungi	1
HP34E	Non-TreM defect	–	Low top mortality	109	SP36X	TreM	Small	Fungi	1
HP34X	Non-TreM defect	–	Low top mortality	9	VP01A	Non-TreM defect	–	Insect holes	4
NC01A	Non-TreM defect	–	Bark wound	40	VP02X	Non-TreM defect	–	Insect holes	3
NC01X	Non-TreM defect	–	Bark wound	5	VP07X	Non-TreM defect	–	Insect holes	1
NC02X	Non-TreM defect	–	Bark wound	6	VP33E	Non-TreM defect	–	Shape defect	1
NC05A	Non-TreM defect	–	Bark wound	2					
NC07A	TreM	Trunk	Canker	31					
NC07E	TreM	Trunk	Canker	6					

Appendix S2. Boxplot of the density of tree-bearing (A) TreMs, (B) Non-TreM defects and (C) No defect in the plots studied according to the species type (broadleaved or coniferous)

Appendix S3. DBH (Mean $\pm$ Standard-error, unit: cm) of tree-bearing TreMs according to TreM class and tree species. Italics indicate values obtained from single observations and blanks, no observation.

Category	Class	All species	Yellow birch	Balsam fir	Paper birch	Red spruce	Red maple
Cavity	Trunk cavity or rot-hole	20,23 $\pm$ 7,78	24,36 $\pm$ 9,4	–	16,72 $\pm$ 3,78	–	17,43 $\pm$ 4,77
	Trunk base rot-hole	20,04 $\pm$ 7,1	22,36 $\pm$ 7,36	12,3 $\pm$ 1,36	15,3 $\pm$ 2,4	23,5 $\pm$ 6,05	17,93 $\pm$ 6,81
Trunk	Canker	17,44 $\pm$ 7,25	31,6 $\pm$ 0	–	14,7 $\pm$ 0	22,06 $\pm$ 7,85	14,61 $\pm$ 5,12
	Bark shelter	17,95 $\pm$ 8,73	24,8 $\pm$ 5,94	9,4 $\pm$ 0	12,8 $\pm$ 0	–	–
	Bark loss	15,13 $\pm$ 5,36	17,38 $\pm$ 7,06	13,61 $\pm$ 3,45	14,14 $\pm$ 5,11	19,65 $\pm$ 7,84	14,25 $\pm$ 3,94
	Large crack	20,59 $\pm$ 8,7	26,01 $\pm$ 10,06	–	13,9 $\pm$ 0	28,84 $\pm$ 13,55	18,51 $\pm$ 6,72
	Fork split	35,75 $\pm$ 6,15	–	–	35,75 $\pm$ 6,15	–	–
Top	Dead or broken branch	19,64 $\pm$ 13,74	34,82 $\pm$ 25,65	11,93 $\pm$ 1,88	15,94 $\pm$ 6,5	10,6 $\pm$ 1,27	20,54 $\pm$ 6,39
	Dead top	14,12 $\pm$ 4,28	15,44 $\pm$ 5,31	12,64 $\pm$ 3,4	12,81 $\pm$ 3,57	15,09 $\pm$ 4,29	16,28 $\pm$ 5,78
.Small	Epicormic shoots	13,4 $\pm$ 0	–	13,4 $\pm$ 0	–	–	–
	Burr	24,65 $\pm$ 10,85	34 $\pm$ 0	15,4 $\pm$ 0	–	32,25 $\pm$ 19,3	20,83 $\pm$ 5,91
	Fungi	19,28 $\pm$ 8,88	23,31 $\pm$ 12,56	23,1 $\pm$ 0	33,3 $\pm$ 0	48,7 $\pm$ 0	17,19 $\pm$ 5,98