Co-occurrence patterns of tree-related microhabitats: A method to simplify routine monitoring

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ARTICLE INFO

ABSTRACT

A Tree-related Microhabitat (TreM) is a distinct, well-delineated morphological singularity occurring on living or standing dead trees, which constitutes a crucial substrate or life site for various species. TreMs are widely recognized as key features for biodiversity. Current TreM typology identifies 47 TreM types according to their morphology and their associated taxa. In order to provide a range of resolutions and make the typology more user-friendly, these 47 TreM types have been pooled into 15 groups and seven forms. Depending on the accuracy required and the time available, a user can now choose to describe TreMs at resolution levels corresponding to type, group or form. Another way to more easily record TreMs during routine management work would be to use co-occurrence patterns to reduce the number of observed TreMs required. Based on a large international TreM database (2052 plots; 70,958 individual trees; 78 tree species), we evaluated both the significance and the magnitude of TreM co-occurrence on living trees for 11 TreM groups. We highlighted 33 significant co-occurrences for broadleaves and nine for conifers. *Bark loss*, *rot hole*, *crack* and *polypore* had the highest number of positive co-occurrences (N = 8) with other TreMs on broadleaves; *bark loss* (N = 4) had the highest number for conifers. We found mutually exclusive occurrences only for conifers: *Exposed Heartwood* excluded both *dendrotelm* and *sap run*. Among the four variables we tested for their positive contribution to significant co-occurrences, tree diameter at breast height was the most consistent. Based on our results and practical considerations, we selected three TreM groups for broadleaves, and nine for conifers, and formed useful short lists to reduce the number of TreM groups to assess during routine forest management work in the field. In addition, detecting potential similarities or associations between TreMs has potential theoretical value, e.g. it may help researchers identify common factors favouring TreM formation or help managers select trees with multiple TreMs as candidates for retention.

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1. Introduction

A Tree-related Microhabitat (TreM) is a distinct, well-delineated morphological singularity occurring on living or standing dead trees, which constitutes a crucial substrate for species (Larrieu et al., 2018). Cavities, conks of lignivorous fungi and dead branches are examples of TreMs. TreMs are widely recognized key features of biodiversity (Bütler et al., 2013) and are useful indirect indicators for biodiversity (e.g. Winter and Möller, 2008; Paillet et al., 2018; Basile et al., 2020). Therefore, Asbeck et al. (2021) have suggested using them as a monitoring tool to address biodiversity conservation issues in forest ecosystems.

Larrieu et al. (2018) identified TreMs according to their morphology and their associated taxa and allocated them into 47 types, the most precise category, 15 groups, and seven forms, the more generic category, by following a hierarchical way. Depending on the accuracy required and the time available, a user can choose the suitable level to record TreMs in the field. For example, forest managers can record TreM forms (e.g. cavities l.s.) during tree marking to estimate TreM diversity at the stand scale whereas TreM groups (such as woodpecker breeding cavities) could be applied in routine surveys and inventories like the national forest inventories, while elaborating management plans or for Natura 2000 site evaluations. Researchers could use TreM types (e.g. small, medium or large woodpecker breeding cavities) for more exhaustive scientific surveys (Larrieu et al., 2018).

Another possible way to simplify and speed-up TreM recording during routine management work would be to use non-random TreM co-occurrence patterns (i.e. when TreM distribution on the tree is co-dependent), to reduce the number of types to observe. In other words, managers could use a shorter list of TreMs as a surrogate for the full list that indicate the presence of further TreMs with a high probability. However, TreM co-occurrence patterns are poorly known. Preliminary studies revealed co-occurrence patterns at the tree scale for European beech (*Fagus sylvatica* L.), pubescent oak (*Quercus pubescens*), holm oak (*Quercus ilex*), silver fir (*Abies alba* Mill.) and Douglas fir (*Pseudotsuga menziesii* Franco) (Larrieu and Cabanettes, 2012; Regnery et al., 2013a; Winter et al., 2015; Puverel et al., 2019). However, these studies used databases with a narrow geographical range and a limited number of observed trees. Larrieu and Cabanettes (2012) highlighted, for example, that bark loss and rot-holes co-occur in both beech and fir while other co-occurrences are tree-species specific: rot-holes and saproxylic fungi co-occur only on beech, and dendrotelms and bark loss only on fir. Winter et al. (2015) showed TreM co-occurrence patterns for Douglas fir, e.g. for bark pockets and rot-holes. These results suggest that co-occurrence patterns may be different between broadleaves and conifers.

Besides tree-species, other tree and stand features also influence these co-occurrence patterns. First, a greater diameter at breast height (dbh) increases the probability of TreMs co-occurring on the same tree (e.g. Winter and Möller, 2008; Vuidot et al., 2011; Regnery et al., 2013a; Larrieu et al., 2014; Courbaud et al., 2017; Asbeck et al., 2019). Therefore, dbh is likely to be a crucial driver of co-occurrence patterns. Second, pioneer species such as *Salix* spp., *Populus* spp. and *Betula* spp. are relatively short-lived (Rameau et al., 1993) and individuals often seem to simultaneously bear several TreM types early in their life cycles, especially TreMs linked to reduced competitive ability (e.g. crown deadwood) or early senescence (e.g. conks of polypores). In contrast, small individuals of long-lived, shade-tolerant species such as *Fagus sylvatica* and *Quercus petraea* for broadleaves, or *Abies alba* and *Picea abies* for conifers (Rameau et al., 1993) rarely bear several TreM types simultaneously (e.g. Larrieu et al., 2014). We therefore hypothesized that tree species with distinct life cycles and succession dynamics would show different co-occurrence patterns. Third, the CODIT system (COmpartmentalization of Decay In Trees; Shigo, 1984) describes the reaction of a tree following a trunk injury in order to limit the volume of wood affected by pathogens. Tree species compartmentalize the decay in unique ways and with a range of effectiveness, and exhibit a variety of CODIT profiles. While some species like the oaks can inhibit the spread of pathogens within their organism by creating both chemical and anatomical boundaries (Shigo, 1984), other tree species like the poplars (*Populus* spp.) are less able to protect themselves and wood decay can quickly affect a larger part of the trunk, thus creating, for example, wide rot-holes. We hypothesized that the type of CODIT profile would affect the development of saproxylic TreMs (i.e. those that involve decaying wood) and would therefore influence TreM co-occurrence. Fourth, Winter et al. (2015) showed that management intensity has an impact on TreM co-occurrence patterns for Douglas fir. Although there are propositions for indices to assess management intensity (e.g., Kahl & Bauhus, 2014), the data required to calculate these indices are only seldomly assessed during field measurements. However, the time since the last harvest is often available, at least broadly speaking, and can be used as a proxy for management intensity to quantify its effect on TreM co-occurrence.

Our study focused on living trees and co-occurrence patterns among a set of TreMs at the tree scale. We expected that (i) co-occurrence patterns of TreMs will differ between broadleaves and conifers, and that (ii) tree dbh, time since last harvest (as a proxy for management effect), succession dynamics of tree species and compartmentalization capacity would drive co-occurrence patterns.

The practical outcome of this study was to develop short and manageable lists to efficiently record TreMs during routine field visits. We thus aim to provide forest managers with a practical tool to better take into account the biodiversity associated with TreMs.

2. Materials and methods

2.1. Data

We collected data from a large range of temperate and boreal forests from Northern Iran to Western Europe (Fig. 1; Table 1SM in Supplementary Material). These forests cover a wide range of degrees of naturalness, from regularly harvested stands to primeval forests (see e.g. Commarmot et al., 2013; REMOTE project https://www.remoteforests.org). The datasets from the managed stands cover various forest types and silvicultural regimes and do not focus on TreM-rich stands only. Each dataset provided was standardized according to the TreM typology by Larrieu et al. (2018). However, since the typologies used by the field agents recording the TreMs differed slightly, we were not able to follow exactly the same typology as Larrieu et al. (2018). In order to optimize the available data, we designated eleven TreM subgroups (Table 1), very close to the 15 TreM groups described by Larrieu et al.'s (2018), and discarded several TreM types that were rarely recorded or recorded with protocols that differed too much to be merged (see Table 1 for the TreM types analyzed). In addition, TreMs belonging to the form "Epiphytic and epixylic structures" (Larrieu et al., 2018) - namely bryophytes, lichens, lianas, ferns and mistletoes - were not included since they have been rarely recorded. Finally, the eleven TreM subgroups used, hereafter referred to simply as TreMs, encompassed 24 TreM types.

Overall 70,958 living trees (including 54,740 broadleaves, 16,218 conifers and 78 tree species) from 2,052 plots were used for the calculations. According to Larrieu et al., 2018, TreMs occur on both living and standing dead trees. However, we analyzed co-occurrence in living trees only since snags are not routinely included in tree-marking for harvesting.

2.2. Analyses

All calculations were performed with R v3.0.0 (R Development Core Team, 2018).

2.2.1. Presence/absence of non-random TreM co-occurrences

The data used was an absence/presence matrix for the eleven TreM subgroups, with one row for each tree observed. To quantify the nature
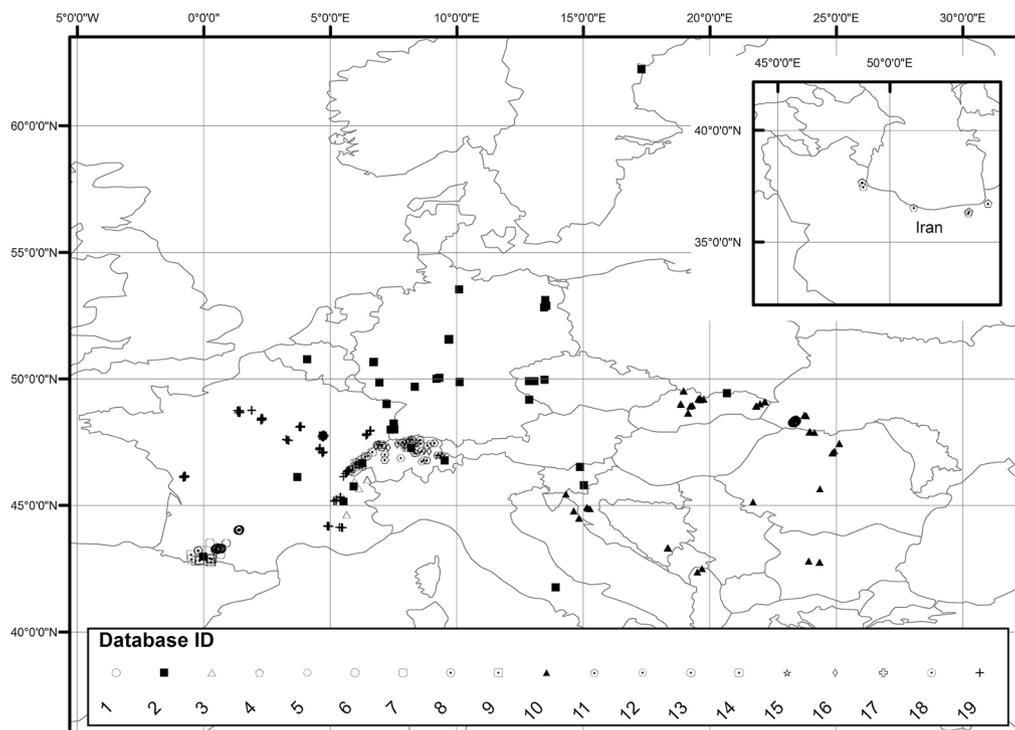
Fig. 1. Map of the TreM datasets; symbols identify the datasets; numbers indicate the dataset IDs shown in Table 1SM.

of a co-occurrence, we counted for the corresponding pair of TreMs (e.g. crack and polypore) the number of (1,1) in the data matrix for the columns associated to this pair (in this example, the first column for crack and the second column for polypore) meaning that both TreMs are present on the same tree; there is no co-occurrence if both TreMs are absent or if only one is present. If this count is low when a TreM is present (e.g. crack) but the other (e.g. polypore) is often absent, the co-occurrence can be qualified as negative; if the count is high since the two TreMs are often both present on the same tree, the co-occurrence can be qualified as positive. To decide if the co-occurrence is significantly positive/negative or random, we compared this count with a similar one calculated on a sample where pairs of 0 and 1 are obtained by resampling on the 0/1 vectors observed for each TreM of the considered pairs independently; so we did a resampling test for each TreM pair. This resampling procedure (the R-script is provided in the supplementary material) gave min, mean and max counts and when an observed count fell inside the min–max interval, the corresponding pair was considered to be random. Otherwise, the co-occurrence was considered non-random (negative or positive). As we observed considerable heterogeneity of presences and co-occurrences at the plot level, we did the resampling at each plot level to tackle specific plot characteristics (number of presences for each TreM and number of trees involved). We ran 10,000 iterations of this resampling. We then calculated, for each pair of TreMs, the difference between the observed co-occurrence frequency (i.e. the count of trees in the database that bore the TreM pair) and the mean frequency obtained by the 10,000 iterations of the resampling; we called this difference "the magnitude of the co-occurrence". The results for broadleaves and conifers were treated separately. Graphical representations (Figs. 2 and 3) were inspired by those provided in the "co-occur" package (Griffith et al, 2016).

2.2.2. Modeling non-random co-occurrences to highlight key factors

To analyze the effect of four explanatory variables (detailed below) on the probability of co-occurrence for each pair of TreMs at the tree scale, we used for the 42 non-random co-occurrences found (33 for broadleaves and 9 for conifers) a logistic model with a binomial error distribution and a logit link-function (GLMM approach, *glmer* function,

R-package *lme4*; Bates et al., 2015). The dependent variable was a binary variable (presence/absence of co-occurrence) since at least one of the TreMs in the respective combination was present. For each combination of TreMs, we considered only the trees bearing at least one of the TreMs since we were looking for co-occurrence. Excluding trees without TreMs did not affect the binomial distribution of the variable. As explanatory variables, we used: (i) *tree dbh*, (ii) *time since the last harvest* on the plot (five classes: 1- <15 years, 2- from 15 to 30y, 3 - from 30 to 50y, 4 - from 50 to 100y and 5 - unharvested for at least 100y), (iii) *tree-dynamic status* (two categories: *long-lived and shade-tolerant species*, and *pioneer/post-pioneer* together in order to balance tree numbers between categories since post-pioneers were underrepresented in the dataset) according to Rameau et al. (1993), and (iv) *compartmentalization capacity* according to Shigo's, 1984 concept (two classes: weak and high; Gilman, 2011; Oven and Torelli, 1999; Schneuwly-Bollschweiler and Schneuwly, 2012; Dujesiefken and Liese, 2015; Table 5SM). We used the plot identity as a random-effect variable (i.e. (1|SitePlot) since several plots were nested in the same site. Using tree-species succession status instead of simply tree species allowed us to include rarely observed tree species and to follow a functional approach to stand dynamics. It should be noted that *compartmentalization capacity* was not pertinent for conifers in our study since all the conifers we assessed have a high compartmentalization capacity according to the literature. The number of trees distributed among the five value classes of *time since the last harvest* was sometimes very irregular. When the number of trees in a class was too small or equalled zero, the model could not be calculated correctly or did not converge; the variable *time since the last harvest* was therefore removed from the model. We systematically used VIF > 3 (Zuur et al., 2010) as the cut-off point to remove collinear variables (*vif.mer* function).

Thirty-six models were tested for each significant co-occurrence and that separately for broadleaves and conifers (31 for broadleaves and 5 for conifers). We then used the *MuMIn* package (Barton, 2019) to calculate the Second-order Akaike Information Criterion and R^2 values (*r.squaredGLMM* and *r.squaredLR*) for each of the 36 models. The significance of each explanatory variable was tested with the *Anova* function (R-package *car*; Fox and Weisberg, 2011). The significance of the different levels of the factorized variables was calculated with the *model.*

Table 1

TreM forms, groups, subgroups (level created for this study to optimize available data) and types (from Larrieu et al., 2018, and Kraus et al., 2016 for the illustrations); TreMs belonging to the form "Epiphytic and epixylic structures" (Larrieu et al., 2018) were not included.

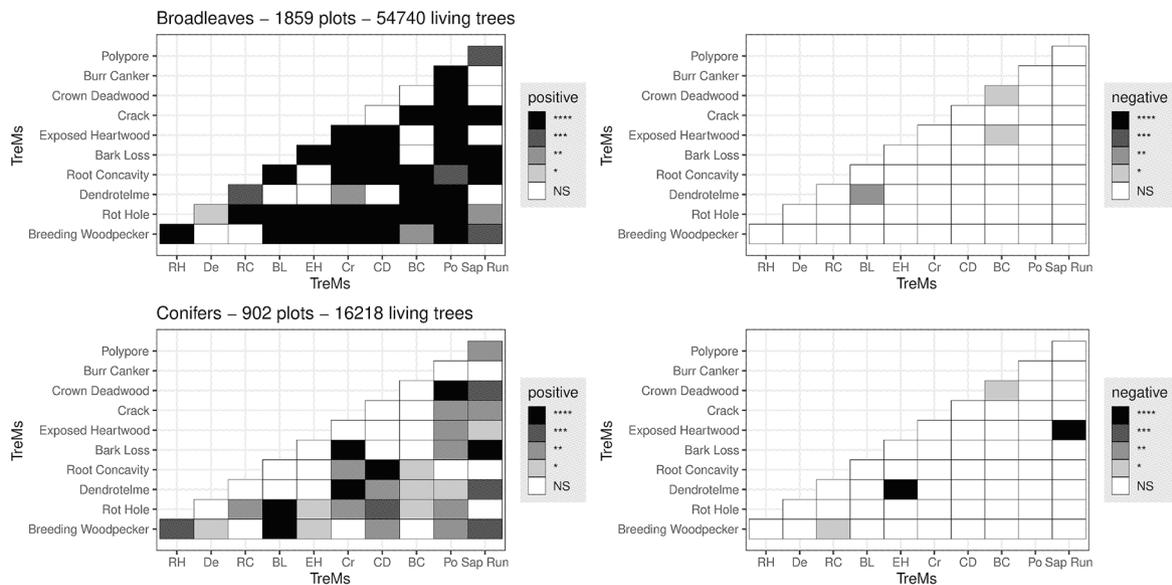| Form	Group	Sub-group	Subgroup definition	Types				
Cavities l.s.	Woodpecker breeding cavities	Breeding.Woodpecker.Hole	Completed woodpecker breeding cavity, fresh or old	Small woodpecker breeding cavity (Opening ø<4cm)	Medium-sized woodpecker breeding cavity (Opening ø=4-7cm)	Large woodpecker breeding cavity (Opening ø>10 cm)	Woodpecker "flute" (string of ≥ 3 breeding cavities)	
	Rot holes	Rot.Hole	Cavity containing mould, with or without ground contact	Trunk base rot hole (ground contact) (Opening ø>10cm)	Trunk base rot hole (without ground contact) (Opening ø>10 cm)	Semi-open trunk rot hole (Opening ø>30cm)	Chimney trunk base rot hole (Opening ø>30cm)	Chimney trunk rot hole (Opening ø>30cm)
	Concavities	Dendrotelm	Phytotelmata, water-filled hole. Cup-shaped concavity that, due to its form, retains water until it dries out by evaporation.	Rotted-bottom or bark-lined dendrotelm (Mean opening ø>15 cm)				
		Root.Concavity	Natural bark-lined concavity at the base of the tree trunk formed by the tree roots and the soil. No mould inside	Root buttress concavity (Entrance ø>10cm; depth>10cm; roof slope <45°)				
Tree injuries and exposed wood	Exposed sapwood only	Bark.Loss	Loss of bark exposing sapwood only. Skinning caused e.g. by felling, skidding, natural tree fall, rock fall, rodents or lagomorphs. Exposed wood at decay stage 1, 2 or 3	Bark loss (Area>300cm² = A5 format)				
	Exposed sapwood and heartwood	Exposed.Heartwood	The stem or a main limb has broken off but the tree is still alive. The wound is surrounded by living wood with sap flow.	Stem breakage (Stem ø>20 cm at the broken point)	Limb breakage with trunk heartwood exposed (Area of exposed heartwood > 300cm² = A5) format)			
		Crack	Simple or splintered crack through both the bark and the wood caused by e.g. lightning strike, frost or wind	Crack (Length>30cm; width>1cm; depth>10 cm)	Lightning scar (Length>30cm; width>1cm; depth>10 cm			
Crown deadwood	Crown deadwood	Crown.Deadwood	Perched deadwood, sun-exposed or not. When a limb has broken off, injury does not affect the trunk	Dead branches (Branch ø>10cm, or branches ø>3cm and >10% of the crown is dead)	Dead top (ø > 10cm at the lower part of the piece of deadwood)	Remaining broken limb (Limb ø>20cm at the broken end; length of the remaining piece >0,5m)		
Excrescences	Burrs and cankers	Burr.Canker	Proliferation of cell growth with rough bark. Sapwood sometimes exposed	Burr (ø > 20 cm)	Canker (ø > 20 cm)			
Fruiting bodies of saproxylic fungi and slime molds	Perennial and ephemeral fungal fruiting bodies	Polypore	Fruiting bodies of annual or perennial polypores, lasting from several weeks (elastic and soft conk, only one layer of tubes) to several years (tough conk showing distinct annual tube layers)	Perennial polypore (Largest ø 5cm)	Annual polypore (Largest ø > 5cm or cluster of > 10 fruiting bodies)			
Fresh exudates	Fresh exudates	Sap.Run	Significant flow of fresh sap	Sap run (Length>10 cm)				

Fig. 2. TreM co-occurrences for broadleaves (top panels) and conifers (bottom panels). The left panels show positive co-occurrences while the right panels show exclusive ones. Although only the results with p < 0.0001 were considered significant, here we show the whole range of significance levels for a broader overview of TreM relationships. X-axis labels are abbreviations of the full names of the TreM-subgroups indicated along the Y-axis, i.e. RH: *rot hole*, De: *dendrotelm*, RC: *root concavity*, BL: b*ark loss*, EH: *exposed heartwood*, Cr: *crack*, CD: *crown deadwood*, BC: *burr canker*, Po: *polypore*. Since plots with mixed stands were counted twice, i.e. for both broadleaves and conifers, total plot number exceeds the total indicated in Table 1SM.
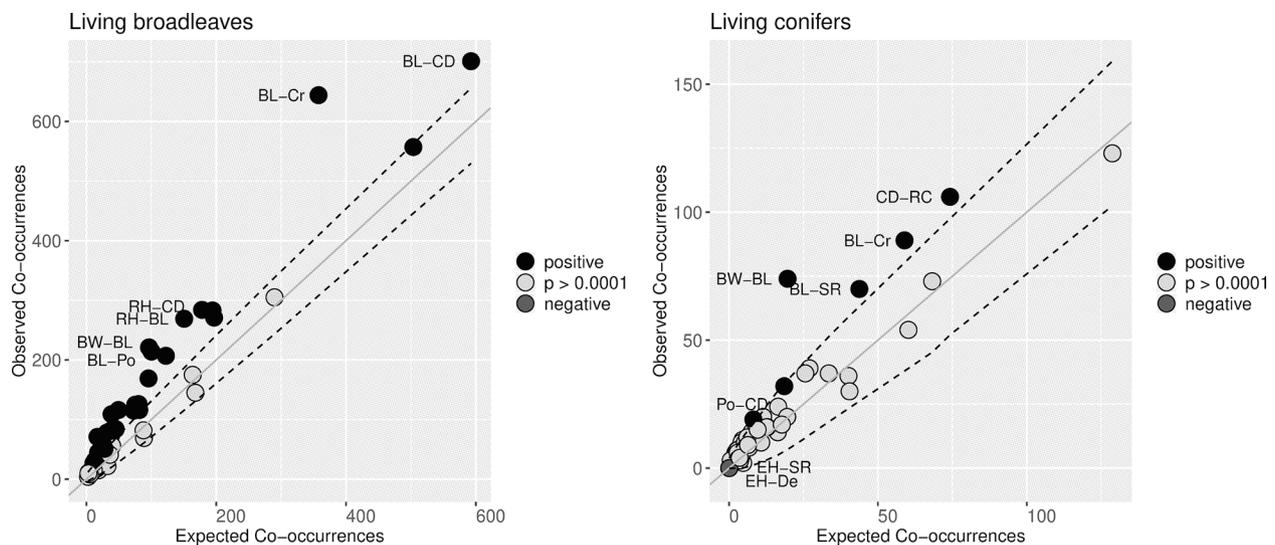

Fig. 3. Magnitude of TreM co-occurrences for broadleaves (left panel) and conifers (right panel). Expected co-occurrence (X-axis) corresponds to the average number of co-occurrences between the 2 TreMs, resulting from a random reallocation of the TreMs observed on each plot over all the trees belonging to that plot. Each dot corresponds to a co-occurrence between 2 TreMs (55 possible pairs). Values along the axes correspond to the number of trees bearing a TreM pair in the whole dataset (for broadleaves and conifers, 1,859 and 902 plots respectively). The dashed black lines delimit the range of values (min and max) calculated for the random assumption (p = 0.0001; see Material and method section). Only the strongest 10% of the magnitudes are identified (see Tables 4SM and 5SM for magnitude values): CD: *crown deadwood*, BL: b*ark loss*, Cr: *crack*, RH: *rot hole*, BW: *breeding woodpecker hole*, Po: *polypore*, EH: *exposed heartwood*, SR: *sap run*, De: *dendrotelm*, RC: *root concavity*.

avg function (R-package *MuMIn*) based on the calculation of the conditional average model.

2.2.3. Selecting tree-related microhabitat combinations for monitoring

We used the results obtained on TreM co-occurrence to identify the combinations of TreMs that gave the most complete representation of TreM diversity while reducing the monitoring effort as much as possible. For this purpose, we assigned a score to each combination of TreMs (from one to ten TreMs) based on their co-occurrences with other TreMs and the reliability of their observation. Our reasoning was that a TreM

strongly co-occurring with others could be a proxy indicator for a larger group of TreMs and should therefore have a higher score. In addition, we considered that TreMs with high observational reliability (i.e. no management, season or observer bias highlighted in literature) and a high occurrence rate (i.e. above median) should have higher scores. We calculated two scores for each combination: one for broadleaved trees and one for coniferous trees. We assigned a score of 0 to any combination of TreMs that did not have any significant co-occurrences with any other TreMs. For the other combinations, the total score was the weighted sum of five criteria (see below). Each criterion had a value

between 0 and 1, which reflected the mean of the values for each TreM in the combination (see Table 4SM). We weighted the values to obtain a clear hierarchy among the criteria. Our first criterion was *non-dependence on management*, with a weight of 5. We considered this criterion the most important of all since harvesting can drastically modify both TreM occurrence (Larrieu et al., 2012; Lassauce et al., 2013; Paillet et al., 2017) and their co-occurrence (Winter et al., 2015). The second criterion was *co-occurrence with TreMs not included in the combination*, with a weight of 4. We considered this criterion highly important since our main aim was to reduce the number of TreMs to observe. The third criterion was the *number of occurrences in the database*, with a weight of 3. This criterion focused on the most frequent TreMs to increase the probability of observing at least one TreM on the short list whatever the stand; this criterion is also important in terms of data collection and training practitioners in TreM observation. The fourth criterion was *TreM life-span* (i.e. permanent versus temporary) with a weight of 2. This criterion was deemed somewhat less important even though TreM longevity makes year-round observation possible. The fifth criterion was *observer effect* (according to Paillet et al., 2015) with a weight of 1. We included this criterion because the presence of an observer effect in certain field records could lead to stand mischaracterization. We selected the best TreM combinations to create short-lists encompassing from one to ten TreMs. We then analyzed how the total weighted scores of these short lists varied as a function of the number of TreMs making up the list, for conifers and broadleaves separately.

3. Results

3.1. Non-random TreM co-occurrences

We highlighted 33 non-random positive co-occurrences for broadleaves while we found seven positive and two mutually-exclusive co-occurrences for conifers (p < 0.0001; Fig. 2). All the TreMs on broadleaves showed at least one significant co-occurrence with another TreM. *Burr canker* never co-occurred with any other TreMs on conifers. *Bark loss, rot-hole, crack* and *polypore* showed the highest number of positive co-occurrences with other TreMs for broadleaves (N = 8) as *bark loss* (N = 4) did for conifers. We found significant mutually-exclusive co-occurrences only for conifers: *exposed heartwood* with *dendrotelm* and *sap run*. Six co-occurrences were shared by broadleaves and conifers: *Crown deadwood* with *polypore, bark loss* with *sap run, bark loss* with *crack, root concavity* with *crown deadwood, rot hole* with *bark loss*, and finally *breeding woodpecker hole* with *bark loss. Dendrotelm* with *crack* was the only co-occurrence specific to conifers.

We found a wide range of magnitude values, mainly for broadleaves (Fig. 3). The strongest magnitudes were observed for the co-occurrences of *bark loss* with *crack* for broadleaves and *breeding woodpecker hole* with *bark loss* for conifers.

3.2. Key factors for high-magnitude non-random co-occurrences

Among a set of four variables tested for their positive contribution to significant co-occurrences (i.e. *dbh, time since the last harvest, tree-species category* in dynamic succession and *compartmentalization capacity* of the tree species), *dbh* was the variable with the highest consistency. It showed a significant (p < 0.05) effect on the likelihood of two TreMs co-occurring for 88% and 71% of the high magnitude (i.e. the 10% strongest magnitudes) non-random co-occurrences for broadleaves and conifers respectively (Tables 2SM and 3SM). Longer time spans without harvesting (time classes 4 and 5, both above 50 years) favored co-occurrences between *breeding woodpecker hole* and both *bark loss* and *crown deadwood, rot hole* and *crown deadwood, bark loss* and both *exposed hardwood* and *crack* for broadleaves, and co-occurrences between *bark loss* and *crack* for conifers. For broadleaves, a shorter time without harvesting (time class 2, 15–30 years) showed a positive effect on the co-occurrence of *rot hole* with *root concavity* and *bark loss* with *polypore*,

while it had a significant negative effect on co-occurrences between *crown deadwood* and *polypore, bark loss* and *crack, root concavity* and *crown deadwood. Tree-species category* and *compartmentalization capacity* were sometimes collinear. Therefore, we were unable to evaluate their contribution for all the co-occurrence combinations. However, for broadleaves, *tree-species category* in dynamic succession did have a significant, though sometimes opposite, effect for half of the co-occurring pairs. For example, *breeding woodpecker hole* had a mainly positive effect – often of high magnitude, as when it was combined with e*xposed heartwood*, but a negative effect among *long-lived and shade-tolerant species* when it was combined with *polypores. Compartmentalization capacity* had a significant effect for pairs including *rot hole*.

3.3. Selecting tree-related microhabitat assemblages for monitoring

The relationship between the scores of the best TreM combinations and the number of monitored TreMs showed a bell-shaped curve both for conifers and broadleaves (Fig. 4). The maximum score was reached quickly for broadleaves, at three TreMs, whereas it was reached much more slowly for conifers, requiring nine TreMs (Table 2).

3.3.1. Broadleaves

For broadleaves, several combinations of only three TreMs showed significant co-occurrences with all the unmonitored TreMs. The assemblage *crack + burr-canker + crown deadwood* had the highest score (Table 2); it displayed strong co-occurrence with unmonitored TreMs and it involved TreMs with relatively frequent occurrences, low sensitivity to management, long life span and low observer effects. This combination score was very similar to the scores obtained by combinations of four TreMs.

3.3.2. Conifers

For conifers, the score increased slowly with the number of monitored TreMs in the combination because co-occurrences were infrequent. Adding a new TreM to the combination did not result in a strong increase in co-occurrence with the remaining TreMs. The maximum score was reached for a combination of nine TreMs: b*reeding woodpecker hole + exposed heartwood + polypore + root concavity + rot hole + sap run* in addition to the three TreMs selected above for broadleaves (Table 2). Adding *dendrotelm* to this combination decreased the overall score because of the sensitivity of *dendrotelm* to management.

4. Discussion

Based on a large-scale database combining 11 TreM groups, we showed significant high-magnitude co-occurrences between TreMs at the tree scale. We also showed that these co-occurrences are more frequent on broadleaves than on conifers, and that dbh had a consistent effect on the co-occurrence, while life traits of trees (i.e. category in dynamic succession and compartmentalization capacity) and forest management had a lesser effect.

4.1. Co-occurrence between TreMs vary with tree species groups

Most of the co-occurrences between TreMs on broadleaves are likely due to the propensity of some species to form certain types of microhabitats (e.g. *crown deadwood* in oaks, Paillet et al., 2019) that may, in turn, lead to the occurrence of other TreMs linked to the same process (in this case: *crack* and *bark loss*; Larrieu, 2014). More generally, the vital status of a given tree is known to be a strong driver of microhabitat dynamics (e.g. Vuidot et al., 2011; Larrieu and Cabanettes, 2012). We can assume that when the vitality of a tree decreases, TreMs linked with the decaying process appear (i.e. saproxylic TreMs). The patterns of co-occurrence we observed in this study, where we worked only with living trees, confirm this assumption. We found mutually-exclusive co-occurrences for conifers only. This is in accordance with the results of Winter
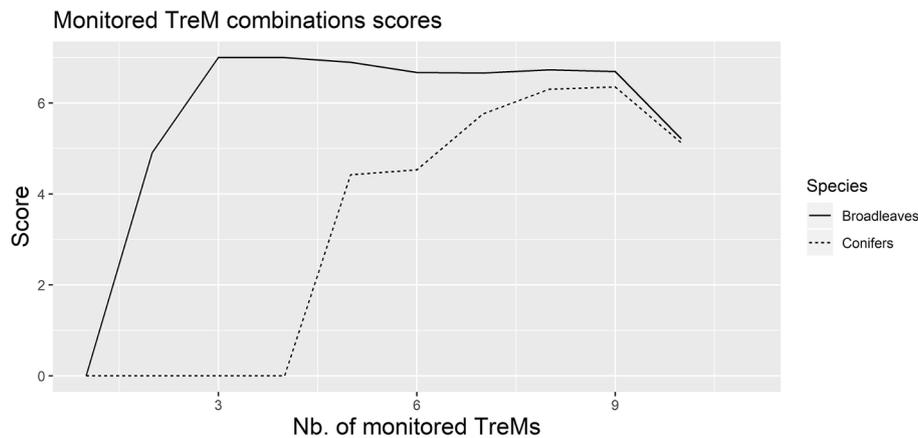
Monitored TreM combinations scores

Fig. 4. Scores of monitored TreM combinations. The score of the best combination of monitored TreMs is shown for different numbers of monitored TreMS, for broadleaves (solid line) and conifers (dotted line).

Table 2
Best TreM assemblages revealing potential candidates for a short list of TreMs for monitoring as a proxy for the set of the 11 TreMs studied; for the calculation of the combined score, see Materials and Methods.

Broadleaves	Number of TreMs observed	Best assemblages (i.e. highest total scores)	Total score
	2	crack + polypore	4.911
	3	crack + burr canker + crown deadwood	7.004
	4	crack + burr canker + crown deadwood + exposed heartwood	7.003
	5	crack + burr canker + crown deadwood + exposed heartwood + root concavity	6.898
	6	crack + burr canker + crown deadwood + exposed heartwood + root concavity + sap run	6.672
	7	crack + burr canker + crown deadwood + exposed heartwood + root concavity + sap run + polypore	6.662
	8	crack + burr canker + crown deadwood + exposed heartwood + root concavity + sap run + polypore + breeding woodpecker hole	6.733
	9	crack + burr canker + crown deadwood + exposed heartwood + root concavity + sap run + polypore + breeding woodpecker hole + rot hole	6.694
	10	crack + burr canker + crown deadwood + exposed heartwood + root concavity + sap run + polypore + breeding woodpecker hole + rot hole + dendrotelm	5.212
Conifers	5	burr canker + crack + crown deadwood + exposed heartwood + bark loss	4.425
	6	burr canker + crack + exposed heartwood + polypore + root concavity + bark loss	4.532
	7	burr canker + crack + breeding woodpecker hole + crown deadwood + exposed heartwood + rot hole + sap run	5.759
	8	burr canker + crack + breeding woodpecker hole + exposed heartwood + polypore + root concavity + rot hole + sap run	6.304
	9	burr canker + crack + breeding woodpecker hole + exposed heartwood + polypore + root concavity + rot hole + sap run + crown deadwood	6.353
	10	burr canker + crack + breeding woodpecker hole + exposed heartwood + polypore + root concavity + rot hole + sap run + crown deadwood + dendrotelm	5.124

et al. (2015) who only found a slightly exclusive co-occurrence between bark pockets and broken tree parts on Douglas fir (*Pseudotsuga menziesii* Mirb. Franco) while studying TreM co-occurrence patterns in European Beech (*Fagus sylvatica* L.) and Douglas fir forests. Although our TreM group *exposed heartwood* is quite similar to the group *broken tree parts* used by Winter et al. (2015), we could not consolidate the two results since we were not able to analyze bark pockets through our database. At the same level of significance (p < 0.0001), our results were in accordance with co-occurrences highlighted by Larrieu and Cabanettes (2012) for (i) European beech, between *rot hole* and *root concavity*, and (ii) Silver fir, between *bark loss* and *crack*, and *sap run* and *rot hole*.

4.2. Tree diameter mainly drives TreM co-occurrence patterns

The effect of tree dbh on TreM co-occurrence probability had not been evaluated before the present study. For our dataset, dbh was the most relevant variable explaining co-occurrence patterns, both for broadleaves and conifers. Generally, the larger the tree, the greater variety of TreMs it bears (e.g. Larrieu and Cabanettes, 2012; Paillet et al., 2019). Thus, a larger dbh favors TreM co-occurrence both "by sampling" (larger trees have more chances to have several types of microhabitats) and by ontogeny (the same processes apply for different TreMs). Dbh is used as a proxy of tree-age since it is easier to record in the field than age. However, several TreMs might be linked with age rather than with dbh since they are more likely to occur over a long period, e.g. polypores (Boddy, 2008). Certain TreMs such as lightning scars might benefit from both age and dbh since lightning strikes on trees are quite rare in temperate forests and a large dbh often accompanies tree dominance and canopy exposure. Finally, TreMs such as woodpecker breeding holes require trees large enough to provide adequate trunk volume (Rolstad et al., 2000). Moreover, the ontogenic stage of the tree (i.e. juvenile, adult, mature and senescent, based on the number of replications of the species-specific architectural unit, which is only slightly correlated to age) can lead to TreM occurrence since e.g. the senescent stage is characterized by the presence of sun-lit dead branches. Therefore, the link between dbh and TreM co-occurrence might actually hide the real links with age or ontogenic stage (Rutishauer et al., 2011). For the few TreM co-occurrences that could be assessed, we found mostly positive effects for a longer time without harvesting, though there were three significant negative effects for TreMs that are rare in managed stands, such as *polypore* and *crack*. Management might reduce co-occurrence for these TreMs in several ways: (i) applying a low-rotation dbh is likely to reduce the number of large trees in the stand (e.g. Asbeck et al., 2019); (ii) TreM-bearing trees are often marked to be cut, thus reducing their proportion (Winter and Möller, 2008, Larrieu et al., 2012), particularly in broadleaf-dominated

stands (Larrieu et al., 2014); and (iii) managers tend to eliminate trees with trunk-borne TreMs, which strongly reduce the tree commercial value, as is the case for *polypores*, since a conk indicates that the wood is already decaying (Stokland et al., 2012) and is therefore unsuitable for timber. All of these choices lead to a reduction in TreM diversity (Larrieu et al., 2012) and thus, mechanistically, the the reduction of co-occurrences. Winter et al. (2015) showed that management affects TreM occurrence patterns in European Beech (*Fagus sylvatica* L.) and Douglas fir (*Pseudotsuga menziesii* Mirb. Franco) forests by strongly reducing the number of significant co-occurrences. Furthermore, they found that management promotes co-occurrences not observed in more natural unmanaged forests; these combinations include cavities and broken tree parts or bark pockets and bark injuries for beech, and broken tree parts and bark injuries for Douglas fir (see Winter et al., 2015 for TreM definitions). In our case, it seems that management – through *time since the last harvest* – has relatively moderate effects.

To date, no studies have investigated the relationship between tree-species life-traits and TreM co-occurrence. It is well known that all woodpeckers excavate their breeding cavities in the part of the trunk degraded by fungi (Schepps et al., 1999; Jackson and Jackson, 2004; Matsuoka, 2008; Zahner et al., 2012). The Black woodpecker (*Dryocopus martius*) may even trigger the colonization by the fungi, thus facilitating cavity drilling (see e.g. Puverel et al., 2019). Therefore, woodpecker breeding cavities and fungi are linked through functional processes. However, conks of fungi may appear several years after the tree has actually been colonized by the mycelium (Conner et al., 1976; Jackson and Jackson, 2004) and thus shift the visible co-occurrence in time. Pioneer broadleaves are often used by woodpeckers as breeding trees, particularly birches (*Betula* spp.; e.g. Pakkala et al., 2019) and poplars (*Populus* spp.; e.g. Hebda et al., 2017). This may be due to the fact that they are susceptible to saproxylic fungi rather early in their life cycle. They also have a weak compartmentalization capacity (see Table 5SM), which allows the fungus, once introduced, to spread quickly inside the wood (Kahl et al., 2017). These traits favor the creation of a large volume of favorable substrate for breeding holes.

For a tree, investing in defence against pathogens is a trade-off with growth speed and life span (Loehle, 1988). Fast-growing broadleaved pioneers, for example, are good at colonizing open areas and competing with low ground/shrub vegetation, but they generally have a weak compartmentalization capacity since their investment in defence barriers is very low and they are short-lived (Morris et al., 2016). The strong relationship between tree-species succession dynamics and compartmentalization capacity explains why we often found colinearity between these variables in our models. We revealed a significant positive effect of a weak compartmentalization capacity for the TreM pair *rot hole/bark loss*. This suggests that most bark loss leads to the development of a rot-hole for broadleaved pioneers, since these trees are not able to isolate the wound area effectively. However, another process might be involved since we found no significant difference between pioneers and long-lived and shade-tolerant tree species for the co-occurrence of this TreM pairs as a function of dbh (Fig. 1 SM).

5. Conclusion: Limitations and fields of application

5.1. TreM co-occurrences as clues to better understanding TreM formation processes

Studies viewing TreMs as key features for biodiversity at the stand level are quite recent (Winter and Möller, 2008). Current knowledge of TreM formation and dynamics is limited and is based only on expertise or cross-sectional (synchronic) data (see e.g. Courbaud et al., 2017). However, there is no doubt that certain TreMs are linked through dynamic processes; for example, we found a positive co-occurrence between *bark loss* and *rot hole* both for broadleaves and conifers. Indeed, *bark loss* will irrevocably evolve towards a *rot hole* if the wound favors infection by wood-decomposing fungi and if the bearing tree is not able

to overlay the wound. Although TreM life spans may be very different (ranging from a few weeks for myxomycetes to several decades for large rot-holes), TreMs evolve slowly on average. Therefore, obtaining diachronic data would require both permanent plots dedicated to this topic and long-term funding for periodic monitoring hard to imagine given the area and time required to obtain enough trees in a dbh range equivalent to the one in our synchronic data. In this context, TreM co-occurrence patterns might help to identify certain TreM dynamic relationships (e.g. shift of dominance between two TreMs when tree-dbh increases), or at least to identify local conditions that lead to the formation of different TreMs on a given tree. These patterns could guide specific studies, as improved knowledge of TreM dynamics may lead to better management of a continuous TreM supply, both at the stand and forest levels.

Despite the large number of trees in our database, it was not possible to perform analyses at the TreM-type level since some TreMs were rarely recorded. Furthermore, due to the heterogeneity of the TreM definitions in the available datasets, we were also unable to analyze all the TreM groups *sensu* Larrieu et al. (2018). Further research should analyze co-occurrence patterns on standing dead trees since they significantly bear TreMs (Larrieu and Cabanettes, 2012; Vuidot et al., 2011; Regnery et al., 2013a; Paillet et al., 2017). However, thanks to the size of our database and the conservative approach we used (significance with a p-value < 0.0001), our results can benefit forest managers during routine practices (tree-marking, inspection visits or plot assessments) or can provide input for management planning based on sound and robust scientific data.

5.2. A short list of TreMs for monitoring based on co-occurrence patterns

Monitoring based on a limited number of TreMs inevitably diminishes the practitioner's ability to precisely assess the full TreM diversity in a forest. However, the best-performing TreM lists we selected (three TreMs for broadleaves and nine TreMs for conifers) are characterized by a strong co-occurrence with unmonitored TreMs. The presence of these TreMs in a forest therefore indicates that TreM richness is probably high in this forest.

Firstly, knowing co-occurrence frequencies can help managers develop efficient strategies for the retention of TreM-bearing trees (habitat-trees; Bütler et al., 2013). Indeed, if co-occurrence frequency is high, managers may be able to conserve a wide range of TreM types simply by protecting the habitat-trees which bear multiple TreMs. In contrast, if co-occurrence frequency is low, managers must retain different habitat-trees for each TreM type, or to target the habitat-trees bearing the rarest TreMs.

Secondly, since practitioners often have limited time for tree marking, reducing the number of TreMs to be monitored could help forest managers incorporate TreM observation and recording, a time-consuming process (Cosyns et al., 2019). Since every TreM has a minimum required size for recording (Larrieu et al., 2018), shorter TreM lists/TreM guides with only a few threshold size values to remember may make TreM assessment more efficient and may also lead to higher acceptance to do such assessments. However, if practitioners use a TreM short-list rather than a more comprehensive one, they must be careful not to reduce the time they dedicate to observing the trees. Since the listed TreMs are not only important *per se* but are also surrogates for other TreMs, missing them inadvertently could lead to significant information loss and thus a higher likelihood that such a tree may be marked for removal. Paillet et al. (2015) highlighted a significant *familiarity* (i.e. the observer has already observed the TreM) observer effect for *cracks*, for instance, thus highlighting the need for careful training. Using a short list of TreMs for monitoring does not justify reducing the overall number of TreM-bearing trees to retain while marking, since the density of habitat-trees is an important driver for species richness and for species composition for taxa such as saproxylic beetles, polypores, hoverflies, bats and birds (Paillet et al., 2018;

Regnery et al., 2013b; Bouget et al., 2013; Winter and Möller, 2008; Larrieu et al., 2019). Furthermore, actively selecting trees bearing different TreMs is the most efficient way to ensure TreM diversity at the stand scale (Asbeck et al., 2020).

The higher number of TreMs selected for conifers as compared to broadleaves was mainly due to the lower number of co-occurrence pairs observed on conifers. *Breeding woodpecker hole* was selected in our best TreM combination for conifers. This TreM is often targeted for biodiversity conservation or integrative forest management approaches. Thus, many forest managers are used to assessing this TreM in their daily work. Furthermore, *breeding woodpecker hole* is often deemed a keystone feature for biodiversity since a wide range of taxa uses or depends on this TreM (Bobiec et al., 2005; Roberge and Angelstam, 2004). C*rown deadwood* was selected for both broadleaves and conifers. This form of deadwood is crucial for numerous saproxylic taxa (e.g. Bouget et al., 2011) and is very rarely assessed, even during deadwood monitoring (see e.g. Larrieu et al., 2019). Although *bark loss* had a high number of positive co-occurrences with other TreMs for both conifers and broadleaves, it was not selected in our procedure, partly because we assigned a strong weight to the variable *management effect,* and this negatively influenced the score for *bark loss*. Indeed, *bark loss* can be a common feature resulting from timber harversting (Larrieu et al., 2012) since trees are often wounded along skidding trails . This may then lead to a local overestimation of occurrence of other TreMs. Moreover, Paillet et al. (2015) highlighted a double observer effect for *bark loss* (both *recording duration* and *familiarity* effects).

For studies that aim at analyzing the relationship between TreMs and biodiversity at the stand level, we recommend using the TreM-type level to ensure a precise description of the stand; indeed, local conditions can influence co-occurrence patterns and there are many highly specialized species whose habitat cannot be characterized by a group of TreMs.

CRediT authorship contribution statement

Laurent Larrieu: Conceptualization, Methodology, Resources, Writing - original draft. **Alain Cabanettes:** Methodology, Formal analysis, Writing - original draft. **Benoit Courbaud:** Methodology, Software, Formal analysis, Resources, Writing - original draft. **Michel Goulard:** Methodology, Formal analysis, Writing - original draft. **Wilfried Heintz:** Data curation. **Daniel Kozák:** Resources, Writing - review & editing. **Daniel Kraus:** Resources, Writing - review & editing. **Thibault Lachat:** Resources, Writing - review & editing. **Sylvie Ladet:** Data curation, Writing - review & editing. **Jörg Müller:** Resources, Writing - review & editing. **Yoan Paillet:** Resources, Writing - review & editing. **Andreas Schuck:** Resources, Writing - review & editing. **Jonas Stillhard:** Resources, Writing - review & editing, Resources, Writing - review & editing. **Miroslav Svoboda:** Resources, Writing - review & editing.

Declaration of Competing Interest

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

Acknowledgments

Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.ecolind.2021.107757.

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