



Key factors determining the presence of Tree-related Microhabitats: A synthesis of potential factors at site, stand and tree scales, with perspectives for further research

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ABSTRACT

Tree-related microhabitats (TreMs) have been identified as key features for forest-dwelling taxa and are often employed as measures for biodiversity conservation in integrative forest management. However, managing forests to ensure an uninterrupted resource supply for TreM-dwelling taxa is challenging since TreMs are structures with a limited availability, some of which are triggered by stochastic events or require a long time to develop. At the tree scale, the role of tree species, diameter at breast height (dbh) and status (i.e. living vs standing dead) for favouring TreM occurrence has been quantified and modelled in several studies, since these tree features are routinely recorded in the field. However, TreM occurrence remains difficult to predict, hampering the elaboration of applicable management strategies that consider TreMs. Using an international database encompassing 110,000 trees, we quantified the explanatory power of tree species, dbh, status, time since last harvest and plot context for predicting TreM occurrence at the tree level. Plot context is so far a “black box” that combines local environmental conditions, past and current management legacies, with local biotic features that have high explanatory power for predicting TreM occurrence. Then, based on the literature, we established a set of 21 factors related to site, stand and tree features for which there is a strong assumption that they play a key role in TreM formation. Finally, we identified a sub-set of nine features that should be recorded in the future to provide additional information to enable better prediction of the occurrence of particular TreMs: (i) at plot level: slope, exposure, altitude and presence of cliffs; and (ii) at tree level: bark features, phyllotaxis and compartmentalization capacity of the tree species, plus ontogenetic stage and physiological state of the individual tree sampled.

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1. Introduction

A Tree-related Microhabitat (TreM) is defined as “a distinct, well-delineated structure occurring on living or standing dead trees, that constitutes a particular and essential substrate 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 support a wide array of biodiversity (see Table 2 in Larrieu et al., 2018) that is not usually supported by other forest structures, such as deadwood items (Stokland et al., 2012). Several studies have highlighted the significant impact of an increase in TreM-bearing tree (hereafter called habitat-tree) density on species richness for several taxa (see e.g. Bouget et al., 2013, 2014a,b, Larrieu et al., 2019, and Winter and Möller, 2008 for saproxylic beetles; Regnery et al., 2013a; Paillet et al., 2018 for bats and birds; Larrieu et al., 2019 for polypores and hoverflies; Basile et al., 2020 for insects and bats). Hence, some authors have suggested using TreMs as indirect biodiversity indicators in forest ecosystems and as tools to promote integrative forest management (Kraus and Krumm, 2013; Winter and Möller, 2008, Regnery et al., 2013b, Paillet et al., 2018; Bütler et al., 2013; Larrieu et al., 2018; Asbeck et al., 2021). However, at plot and stand scales, the relationship between TreM density and/or diversity with variations in biodiversity are not so straightforward. Indeed, this relationship is only partially consistent, for both species’ richness and composition, when considering a range of forest contexts (Bouget et al., 2013, 2014a,b; Paillet et al., 2018). This is likely due to complex interactions between TreMs and other resources (e.g. deadwood items, flowering plants in clearings, water bodies; Larrieu, 2014), flaws in procedures for assessing taxa and TreMs (Larrieu and Bouget, 2017), time lags in the response of certain TreM-dwelling species to TreM presence (Herrault et al., 2016), as well as the spatial distribution of source populations (Komonen and Müller, 2018).

The spatial distribution of TreMs is not solely dependent on that of the TreM-bearing trees. Indeed, they are typically limited in availability, persisting from only a few days for lignicolous agarics, to several decades for large rot-holes. Thus, TreMs can be considered as Ephemeral Resource Patches (ERP, Finn, 2001). Furthermore, some of these structures are generated by stochastic events that occur very rarely (e.g. lightning scars), or have a very long development time (e.g. fully evolved rot holes). Numerous forest-dwelling species are continuity-dependent and therefore are restricted by both development time of a novel habitat and the time required to colonize that novel resource patch (Nordén et al., 2014). As a result, it is challenging to manage forests to ensure a continuous resource supply for TreM-dwelling taxa. To provide forest managers with practical recommendations for the conservation of TreM-dwelling taxa, i.e. which trees should be exempt from harvesting, numerous studies have attempted to identify key features at the tree level that are linked to TreM formation. They have highlighted the key roles of tree species, tree diameter at breast height (dbh) and status (i.e. living vs standing dead) for driving the occurrence and abundance of TreMs (Winter and Möller, 2008; Michel and Winter, 2009; Vuidot et al., 2011; Regnery et al., 2013b; Larrieu and Cabanettes, 2012; Larrieu et al., 2014b; Paillet et al., 2018, 2019; Kozák et al., 2018; Asbeck et al., 2019). Notwithstanding the abundance of studies on the topic, to date, predictive models have mainly focused on only two basic tree features, namely dbh and species for living trees (Courbaud et al., 2017; Jahed et al., 2020); in some cases, a qualitative variable was used to separate managed and unmanaged forests (Courbaud et al., 2022). Dbh and tree-species are easy to record, and are also routinely assessed by forest managers for silvicultural and monitoring purposes. However, the power to predict TreM occurrence with these two tree features alone is often rather low, e.g. about 26 % in beech (*Fagus sylvatica*)-silver fir (*Abies alba*) forests (Larrieu et al., 2014a). Moreover, Courbaud et al. (2022) have shown that site effects are huge. However, these previous works have not been able to highlight what site features influence the presence and dynamics of TreMs.

For these reasons, the distribution of TreMs is currently difficult to

predict, hampering the elaboration of appropriate management guidelines that take into consideration these crucial biodiversity features. This is particularly important as the need to take TreMs into account in silvicultural planning is increasingly acknowledged among forest managers. For example, TreMs have been incorporated into an index that is routinely used in the field by forest managers in France (Index of Biodiversity Potential, IBP; Larrieu and Gonin, 2008; Gosselin and Larrieu, 2020). At a larger spatial scale, a rapidly growing network of about 160 training plots (called “marteloscopes”) has been established across 22 countries, mainly in Europe, with the aim of improving managers’ knowledge about TreMs and inventory calibration, employing tree-marking exercises in the field (Kraus et al., 2021). Therefore, there is a critical need to better explain and predict TreM occurrence and the processes that lead to their formation, with the ultimate aim of encouraging forest managers to take TreM-associated biodiversity into account in their daily work routines.

In this paper, using a large international TreM database, we first quantify the explanatory power of the factors that currently feature in most of the available datasets, namely tree species, dbh, tree status (i.e. living or standing dead), time since last harvest and plot context for predicting TreM occurrence at the tree level.

Plot context is currently a “black box” which combines local environmental conditions, past and current management legacies, and local biotic features which might impact TreM formation in several ways. Environmental conditions determine tree species assemblages in relation to both biogeographic and bioclimatic contexts, as well as soil fertility. Soil fertility may determine the presence of epiphytic plants that are considered as TreMs when they climb on trunks. For example, ivy (*Hedera helix*) does not thrive on very acidic and nutrient-poor soils (Dumé et al., 2018). Thin soils which are prone to be often dry can promote dead wood in the crown of the trees (Breda et al., 2004). Furthermore, the dynamics of TreM formation has been shown to differ between tree species (Courbaud et al., 2017; Jahed et al., 2020) and not all tree species are likely to support the same type of TreMs (Vuidot et al., 2011; Larrieu and Cabanettes, 2012; Paillet et al., 2019). The presence of particular geological features, such as cliffs or mobile scree, may increase the density of trees that have bark loss or broken stems due to falling rock (Dorren and Berger, 2006; Stokes et al., 2005). For example, in the Black Forest (Germany), Asbeck et al. (2019) highlighted that increasing altitude favours the number of buttress-root concavities and epiphytic lichens, while mosses and mistletoe are more abundant at lower altitudes. However, the detailed effect of local conditions has, to date, not yet been well quantified. Furthermore, such observations may actually mask confounding effects, e.g. when altitude and slope are strongly and positively correlated, as is often the case in mountain areas. Forest management is known to influence both the density and the diversity of TreMs (e.g. Winter and Möller, 2008; Larrieu and Cabanettes, 2012), while the impact of harvesting persists over the long term (Bouget et al., 2014a,b; Paillet et al., 2015; Larrieu et al., 2016). In addition, certain biotic features may have an effect on the presence and abundance of TreMs, e.g. density of red deer (*Cervus elaphus*) in relation to food resource availability for bark loss (Verheyden et al., 2006), or the presence of black woodpecker (*Dryocopus martius*) for both breeding holes and feeding concavities (Bobiec et al., 2005).

Hence, secondly, in order to unpick the composition of this black box and to identify the most influential features, we consider a set of factors related to site, stand and tree features for which there is a strong assumption that they play a key role in TreM formation. The main goal here was to identify the most biologically relevant drivers, rather than relying on only the most widely available variables. An approach based on a selection of factors that have been identified in the literature as likely having a positive influence on TreM occurrence should help us to avoid focusing on spurious indirect relationships with no causal role in TreM formation.

Thirdly, based on a consideration of the trade-off between sampling effort and relevance for explaining the occurrence of TreMs, evaluated

Table 1

Proportion of variance explained by the full and simplified models for predicting the occurrence of tree-related microhabitats (TreM). For each group of TreMs, the full model includes tree diameter at breast height (dbh), tree species, tree status (dead vs. living), time since the last harvest and plot context, as well as several two-way interactions (see Materials and Methods). Plot context integrates local environmental conditions, past and current management legacies, and local biotic features. To evaluate the proportion of variance in TreM occurrence explained by each feature, simplified models were built that excluded each one of these features in turn. The feature that explained the highest proportion of variance for each TreM group is indicated in bold.

TreM group	Total number of trees observed	Full model	Dbh excluded	Tree species excluded	Tree status excluded	Time since last harvest excluded	Plot context excluded
Woodpecker breeding cavities	106,230	0.249	0.208	0.248	0.133	0.246	0.050
Rot holes	106,230	0.378	0.332	0.354	0.354	0.378	0.079
Dendrotelms	86,272	0.150	0.125	0.147	0.101	0.150	0.042
Buttress-root concavities	74,465	0.599	0.508	0.587	0.586	0.598	0.373
Exposed sapwood only	98,945	0.472	0.420	0.464	0.317	0.472	0.192
Exposed sapwood and heartwood	90,758	0.222	0.177	0.215	0.146	0.221	0.019
Cracks	98,945	0.265	0.225	0.259	0.213	0.264	0.045
Crown deadwood	99,486	0.516	0.456	0.507	0.483	0.516	0.119
Burrs and Cankers	88,273	0.181	0.118	0.174	0.175	0.181	0.049
Perennial polypores	99,670	0.424	0.364	0.421	0.188	0.424	0.185
Sap runs	90,930	0.170	0.126	0.159	0.159 *	0.168	0.004

* Resulted from an exceptional bad fit that could not be improved.

from both literature and based on our own expertise, we suggest a subset of features that i/ should be tested by further studies focusing on TreMs when widely available (e.g. via large scale databases), or ii/ should be recorded in the future by researchers in the field.

2. Material and methods

2.1. Predictive power of the features currently available in most TreM datasets

To quantify the predictive power of the features shared by most of the datasets, we used an international database which integrates 23 harmonized datasets, comprising 100,855 living trees and 10,354 standing dead trees belonging to 89 tree species (appendix; Table 1SM). For each of the eleven TreM subgroups that were designated by Courbaud et al. (2022), we built a Generalized Linear Mixed Model (GLMM) that described the presence/absence of this TreM group in relation to dbh, tree species, tree status (living/standing dead), plot context, and time since the last harvest (four categories: <20y, 21-50y, 51-100y and >100y). Three two-way interactions - namely dbh with status, dbh with time since last harvest, status with time since last harvest - were also included as fixed effects. Interactions of plot context and tree species with dbh and status were included as random effects. The interaction between plot context and tree-species was considered as redundant and was not included in the models. We then simplified each full model by excluding each explanatory factor in turn to quantify its effects in terms of the proportion of variance explained: plot context, dbh, tree species, tree status and time since last harvest. The GLMM models were fitted with a Bernoulli structure (binomial distribution and logit link) to describe presence/absence using the BRMS Package (Bürkner, 2021). The model took into account potential correlation among random effects, with an a priori of no correlation. The a priori distributions were taken as normal $N(0,2)$ for fixed effects, exponential with parameter equal to 1 for variances and the LKJ distribution for correlation matrices, as recommended by McElreath (2020). We used BRMS for the analysis rather than MCMCglmm since it uses the Stan library (Bürkner, 2021) and therefore employs the Hamiltonian MCMC that provides a better exploration of the posterior distribution, generating results that are more robust with a shorter computational time. Note, however, that we also analysed the same set of models using the MCMCglmm approach (Hadfield, 2010) and obtained very similar results. For BRMS, 1000 iterations for the burn in, 2000 iterations for the estimations with 4 chains in parallel were enough to obtain convergence compared to 200,000 iterations for burn in, 400,000 iterations for estimation with thinning of

100 for the MCMCglmm. Since plot context and time since last harvest are mechanistically linked to tree dbh and to the presence/absence of certain TreM groups, models that omitted these two variables were simply considered as a control.

For each explanatory variable, the proportion of variance explained was calculated as the variance explained by that given feature in the corresponding model, divided by the total variance in the presence/absence of the particular TreM group.

2.2. Assessing additional features that may play a key role in TreM formation

Based on a non-comprehensive review of the literature focusing on tree growth, morphological traits of tree-species, as well as physiological and architectural issues, we selected a range of factors that may have an indirect relationship with TreM occurrence by favouring either tree-level singularities or specific stand features. We sorted these factors into three categories: (i) site environmental conditions, (ii) stand features, and (iii) tree features, including species, chronological age and ontogenic stage (Table 2). From the literature and based on the authors' expertise, each feature was evaluated in terms of its potential effect on TreM formation: 'highly probable effect' was assigned if at least one study indicated a strong and explicit effect of that factor on TreM formation, or 'probable effect' if at least one reference reported a probable or indirect effect and the authors' expertise confirmed that this may indeed be the case. We here considered the 15 TreM groups described by Larrieu et al. (2018) as the best compromise between precision and simplicity for analysis (Table 2SM).

3. Results

3.1. Predictive power of the features currently available in the databases

The best full models explained, on average, around one third of the variance in TreM occurrence, from 15% for dendrotelms to 59.9% for buttress-root concavities (Table 1). Plot context was always the feature that explained the highest proportion of variance in TreM occurrence.

3.2. Additional features that may play a key role in TreM formation

From the literature, we identified 21 features which may play an important role in TreM formation: nine environmental site specific, two stand dependent and ten tree-related features (Table 2). The feature implicated in the formation of the highest number of TreMs is the

Table 2
Potential key factors for TreM formation. Effect on TreM formation: *** ‘highly probable’, * ‘probable’.

Scale and Type of factors	Factor	Potential relationship with TreMs	References	TreM group (with types belonging to the group that are likely to be particularly impacted)
Site; Environmental conditions	Unfavourable conditions for tree growth	Direct sun exposure, poor soil and low precipitation, faster ontogenic dynamics	Barthélémy and Caraglio (2007); Nicolini and Caraglio (1994); de Kroon et al. (2005); Pearcy et al. (2005); Sabatier and Barthélémy (1995)	*Crown deadwood *Rot holes *Exposed sapwood and heartwood (Cracks)
	South-facing slope	Increases abundance of Mistletoe	Oliva and Colinas (2010)	*Epiphytic and parasitic crypto- and phanerogams (Mistletoe)
	Altitude	Humid climate favours epiphytic plants	Rameau et al. (1991)	***Epiphytic and parasitic crypto- and phanerogams (Lichen, Liana, Mosses)
	Fertile soil	Favours epiphytic plants	Rameau et al. (1991)	***Epiphytic and parasitic crypto- and phanerogams (Lichen, Liana, Mosses)
		Favours tree species with non-acid barks (e.g. ash, poplars, sycamore)	Rameau et al. (1991)	*Epiphytic and parasitic crypto- and phanerogams (Lichen, Liana, Mosses)
	Thin or compact soils	Favours buttress formation	Ennos (1993)	***Concavities (Buttress root concavities)
		Thin soils favour branch death	Breda et al. (2004)	***Crown deadwood (Dead branches; dead top)
	Wind	Favours buttress formation (reaction wood)	Crook et al. (1997); Fournier et al. (2015)	***Concavities (Buttress root concavities)
		Strong wind events lead to breakages	Gardiner et al. (2000); Petty and Swain (1985)	***Exposed sapwood and heartwood (Stem breakage; Limb breakage; Fork split at the intersection)
	Cliffs	Cliffs up slope or mobile scree favour wounds and stem breakage by stone impacts	Dorren and Berger (2006); Stokes et al., 2005	***Crown deadwood (Remaining broken limb) ***Exposed sapwood (Bark loss)
	Steep slopes	Favours buttress formation (reaction wood)	Fournier et al. (2015)	***Exposed sapwood and heartwood (Stem breakage) *Concavities (Buttress root concavities)
	Mountain summits and ridges	Locations prone to lightning strikes	López et al. (1995)	*Exposed sapwood and heartwood (Lighting scars)
	Stand; Stand features	High tree density	Favours high trunks without branches	Barthélémy and Caraglio (2007); Nicolini and Caraglio (1994); Nicolini et al. (2000)
		Favours development of accidental forks including bark, prone to fork breakage	Slater (2018)	***Exposed sapwood and heartwood (Fork split at the intersection)
Spatial distribution of trees		Tree clustering is detrimental to cavity digging by woodpeckers	Puverel et al. (2019)	*Woodpecker breeding cavities (Large woodpecker breeding cavity)
Tree; Tree species	Low compartmentalization capacity	Favours fungi and decay	Dujesiefken and Liese (2011); Smith (2015)	***Rot holes
	Presence of heartwood	Heartwood absent in young trees, sometimes for a long period (e.g. 25–70 years for <i>Fagus sylvatica</i>), hinders rot-hole dynamics	Trouy (2015)	*Rot holes
	Phyllotaxis	Greater occurrence of bark embedded in the wood for species with decussate opposite phyllotaxis	Drénou (2000); Stobbe et al. (1998)	Exposed sapwood and heartwood (***Fork split at the intersection; *Crack)
	Tree architecture (forks):	Some architectural models (e.g. Troll’s model; Hallé and Oldeman, 1970) produce recurrent forks with weak anchoring throughout their lifetime (e.g. <i>Ulmus</i> spp., <i>Tilia</i> spp.)	Chomicki et al. (2017); Drénou (2000); Heuret et al. (2002)	*Exposed sapwood and heartwood (Fork split at the intersection)
	Bark features	Rough bark (e.g. <i>Quercus</i> spp., <i>Juniperus</i> spp.) favours formation of bark microsoils	Villarreal and Esteve-Raventos (1999); Halama et al. (2014)	***Microsoils
		High bark pH favours mosses	Fritz et al. (2009)	***Epiphytic and parasitic crypto- and phanerogams (Mosses)
		Smooth and hydrophobe barks are unfavourable to plasmodial slime moulds	Everhart et al., 2009	*Ephemeral fungal fruiting bodies and slime moulds (Myxomycetes)
	Mistletoe	Mistletoe has specific hosts	Norton and Carpenter (1998)	***Epiphytic and parasitic crypto- and phanerogams (Mistletoe)

(continued on next page)

Table 2 (continued)

Scale and Type of factors	Factor	Potential relationship with TreMs	References	TreM group (with types belonging to the group that are likely to be particularly impacted)
Tree; age	Tree age	The probability for the tree to be wounded and infected with decay increases with tree age Young trees have very wet sapwood sensitive to frost	Dujesiefken et al. (2016); Smith (2015) Perré and Badel (2006); Walker et al. (2011) Smith (2015)	***Rot holes *Exposed sapwood and heartwood (Cracks) ***Rot holes
Tree; ontogenesis	Development stage	Compartmentalization capacity decreases as the development stage takes a step forward Development stage is characterized by the establishment of main forks (no accidental forks): young stage = no forks, adult = 1–4 forks, mature = 5–10 forks, senescent > 10 forks Irregularization of the cambial activity during ontogenesis The senescent stage is characterized by sun-exposed dead branches Limited ability to react at the senescent stage The disappearance of the root pivot during senescent stage favours buttress formation	Chomicki et al. (2017); Drénou et al. (2000, 2019); Drénou and Caraglio (2019); Gleißner (1998); Roloff (1988) Larson et al. (1993); Lachaud and Bonnemain (1981); Moss and Gorham (1953) Rutishauer et al. (2011); Gleißner (1998); Roloff (1988) Drénou (1994); Nicolini et al. (2003); Bryan and Lanner (1981); Vesik (2006) Mattheck (1991)	*Concavities (Dendrotelms) * Exposed sapwood and heartwood (Cracks) *Microsoils *Concavities ***Crown deadwood ***Crown deadwood **Exposed sapwood and heartwood *Epiphytic and parasitic crypto- and phanerogams (Lichen, Mistletoe) *Perennial fungal fruiting bodies *Ephemeral fungal fruiting bodies and slime moulds *Concavities (Buttress root concavities)
Tree; Physiological state	Tree physiological state	Impacts both biomechanics of epicormic shoots (weak anchoring) and dead branch presence	Hirons and Thomas (2018); Lebourgeois et al. (2015); Drénou et al. (2015)	***Crown deadwood *Exposed sapwood and heartwood *Perennial fungal fruiting bodies *Ephemeral fungal fruiting bodies and slime moulds

ontogenic stage of the tree, potentially linked to eight TreMs. The TreM groups that were the most likely to be impacted were *exposed sapwood and heartwood* (potentially linked to 10 factors), *epiphytic and parasitic crypto- and phanerogams* (6 factors), *crown deadwood* (5 factors), *rot holes* (5 factors) and *concavities* (4 factors).

4. Discussion

4.1. Features that may play a key role in TreM formation based on biological processes

Ontogenic stage appears to provide more power for predicting TreM formation than tree age. During its ontogeny, a tree goes through four stages of development (Drénou, 2017; Fig. 1): young, adult, mature and senescent. During the young stage, the branching consists of a limited number of axis categories (architectural unit) which is characteristic of each tree species. The branches are both thin and ephemeral, so that they form a temporary crown. The adult stage corresponds to the duplication of the architectural unit specific to each species, with the establishment of main forks that structure the crown. The mature stage is reached after the growth phase, when the tree acquires a definitive crown volume. At this stage, branches continue to develop, but the crown extent does not further increase. The tree's ability to produce replacement shoots then decreases, making crown dislocation irreversible by the progressive death of branches during the senescent stage. The mature and senescent stages account for about 50% of a tree's lifespan (Barthélémy and Caraglio, 2007) and promote the development of crown deadwood, together with TreMs that emerge from wounds, since compartmentalization capacity (Smith, 2015) decreases with

developmental stage (Table 2). The establishment of large forks during the last three ontogenic stages favours the presence of both microsoils (Hertel, 2011) and dendrotelms (Gossner, 2018).

Developmental stage, however, should not be considered equivalent to tree age: very old trees can still be in the mature stage and be able to generate replacement shoots during recovery following stress (Drénou, 2017). Tree diameter is only roughly correlated with age, as it is highly dependent on the tree species and environmental factors such as the fertility of the site, climate or level of competition. Some late-successional tree species, such as silver fir (*Abies alba*) and European beech (*Fagus sylvatica*), can go through a very long-lasting stagnation stage, sometimes for more than one century, when dbh increases only slightly (Pantic et al., 2015; Pavlin et al., 2021). As dbh is much easier to record than age, it is often used in studies based on longitudinal monitoring of individual trees (e.g. Courbaud et al., 2017, 2022). However, it cannot be used as an interchangeable measure of either tree age or ontogenic stage.

4.2. The effect of management is complex and difficult to assess

Forest management manipulates several factors that may influence the occurrence of TreMs: tree species composition (Vuidot et al., 2011; Larrieu and Cabanettes, 2012; Regnery et al., 2013b), tree density (Larrieu et al., 2012, 2014b; Winter et al., 2015), harvesting diameter threshold, the range of tree trunk diameters (Larrieu and Cabanettes, 2012), the proportion of remaining habitat-trees after each cutting operation (Winter and Möller, 2008; Lassauce et al., 2013) and the density of snags (Vuidot et al., 2011; Larrieu and Cabanettes, 2012; Asbeck et al., 2020). Furthermore, harvesting impacts both the density

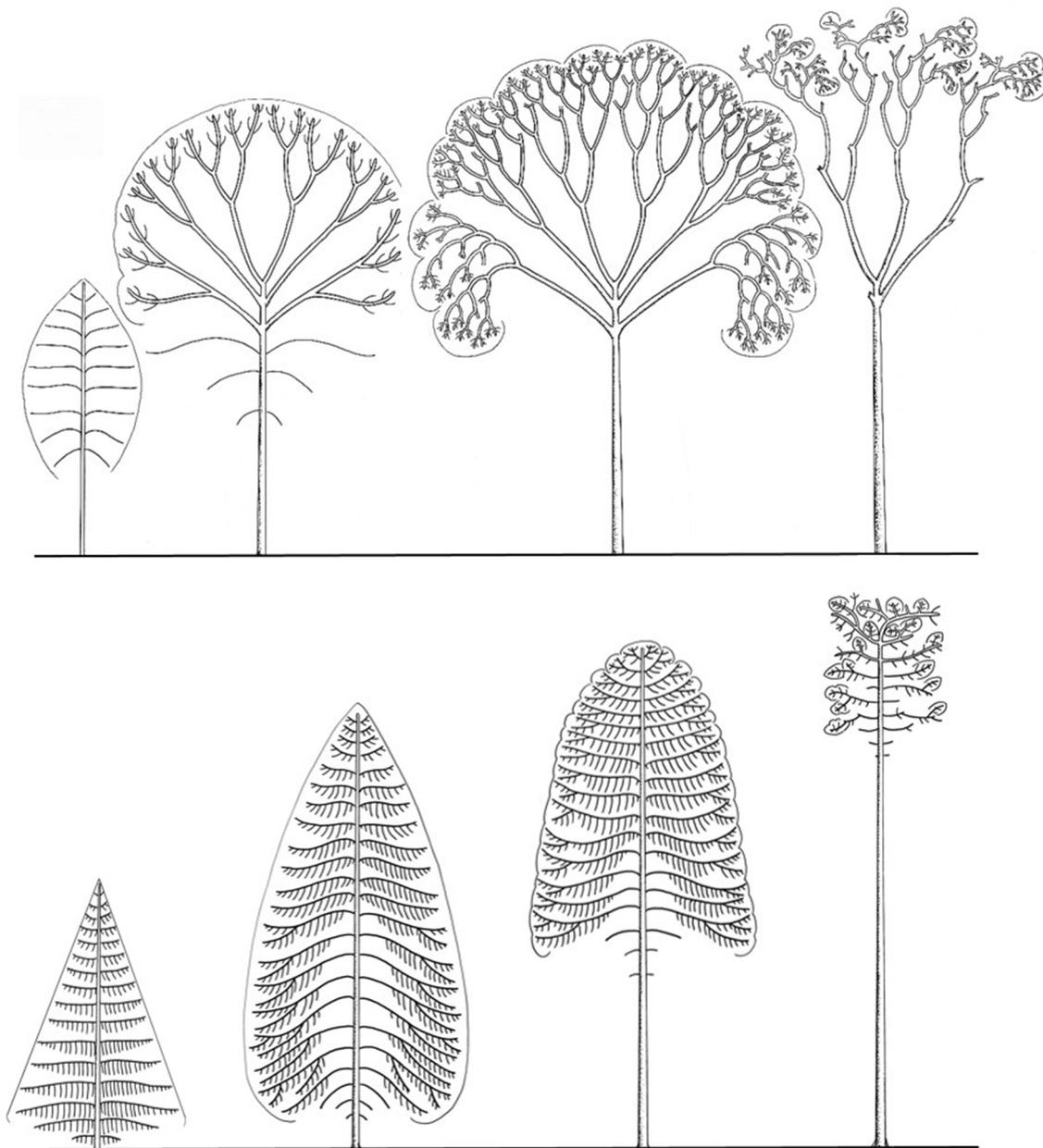


Fig. 1. Ontogenic dynamics of tree growth. Illustration of the four developmental stages (from left to right: young, adult, mature and senescent) for broadleaves (top line) and conifers (bottom line); main features of each stage: (i) broadleaves; Young: crown with pyramidal contour, trunk without fork (except accident); Adult: regular and spherical contour of the crown, 1 to 4 waves of main forks; Mature: “cauliflower” crown contour, 5 to 10 waves of main forks; Senescent: crown contour dislocated, more than 10 waves of main forks; (ii) for conifers; Young: crown with pyramidal contour, linear (not forked) branches; Adult: crown with pyramidal contour, low forked branches; Mature: top of the crown rounded, branches all forked; Senescent: crown top in form of plateau; (original drawings made by CD).

and diversity of TreMs borne by the habitat-trees (Winter and Möller, 2008; Larrieu and Cabanettes, 2012; Paillet et al., 2017; but see Vuidot et al., 2011; Winter et al., 2015). Silvicultural practices that favour the removal of trees with undesirable characteristics likely reduce the density of potential habitat-trees, especially during tending operations in young stands and during thinning through the selective removal of “defect-bearing” trees (Martin and Raymond, 2019). On the other hand, harvesting of trees can create felling and skidding injuries in the remaining trees, or sun-scalds on smooth-bark species (e.g. beech, cherry). Integrated forest management and other retention forestry approaches may selectively spare, protect and promote habitat-trees (Krumm et al., 2020; Kraus and Krumm, 2013).

The most relevant factor with regard to management is likely silvicultural practice, especially in the case of systems using clear-cuts, i.e.

coppice and coppice with standards, and can be deduced from field observations. To better assess management intensity, it would be useful to consider additional information such as type, frequency and intensity of harvesting operations in selective thinning, target diameter in uneven-aged stands, rotation lengths in even-aged stands, application of TreM retention strategies (and target density of habitat-trees) or the use of tending operations in young stands. Also, the harvesting methods and machinery that are used can have a strong impact on tree injuries and subsequent TreM formation. Horse driven tree removal, for example, will have lower impacts on future TreM development as compared to mechanized techniques, but this former method remains rare and limited to sensitive situations (e.g. bogs) since the productivity of horse-driven logging is low. Such additional information can be obtained from forest managers or by consulting management plans and harvesting

Table 3

Assessment of the compromise between recording cost of additional features which might be assessed in future studies and their relevance for explaining the occurrence of Tree-related Microhabitat (TreM) groups; cost: time for recording or technology requiring specific skills; relevance: the number of tree-related microhabitats potentially affected and the magnitude of expected effect.

Grain	Feature	At the laboratory	In the field	Cost	Relevance for explaining the occurrence of TreM groups	Remarks	Trade-off
Stand/ plot	Slope	Digital Elevation Model	Using clinometer	Very low	1 TreM group potentially affected with a low magnitude of expected effect.	Field measurements provide more accurate estimates and incorporate spatial variability.	Fairly good
	Exposure	Digital Elevation Model	Using compass	Very low	1 TreM group potentially affected with a low magnitude of expected effect.	Field measurements provide more accurate estimates and incorporate spatial variability.	Fairly good
	Presence of cliffs	Digital Elevation Model (e.g. selecting slopes over 80°)	Direct observation	Low	2 TreM groups potentially affected; the magnitude of expected effect is very high.	Preliminary investigations in well-studied areas showed this method is not sufficiently sensitive for detecting small cliffs.	Good
	Altitude	Digital Elevation Model	Using altimeter	Very low	1 TreM group potentially affected; the magnitude of expected effect is very high.	Asbeck et al. (2019) showed that increasing altitude favours the number of buttress-root concavities and epiphytic lichens, while mosses and mistletoe are more abundant at lower altitudes.	Good
	Soil fertility	Geological data on GIS	For nutrients: Humus forms, flora, pH at the soil surface layer, or tree size (e.g. by the total height at a given age) when the stand is mature For water storage capacity: recording depth, the proportion of coarse fragments and textures for each layer	High (in the field)	5 TreM groups potentially affected and the magnitude of expected effects are rather high for 3 groups.	Geological data only takes nutrient richness into account and ignores soil water storage; it therefore needs to be complemented by additional datasets focusing on soil hydraulic properties or water balance (e.g. Global Soil Water Balance Geospatial Database; see Trabucco and Zomer, 2010). Observers need to be well trained to use such methods for qualifying soil features in the field. Measuring soil depth quickly requires specialized tools such as an auger and the presence of coarse fragments (even when not abundant) may cause difficulties for penetrating the soil, leading to an underestimation of soil depth.	Bad
Tree	Topographic situations exposed to strong wind or lightning	GIS	Field assessment	Low	3 TreM groups potentially affected by high wind speeds and the magnitude of expected effect is high. 1 TreM group potentially affected by lightning strikes with a low magnitude of expected effect.	Wind speed is very difficult to assess at the stand level even though ridges and passes are more prone to high wind speeds. Dendrochronological data can be used as a proxy for wind exposure by highlighting windthrow disturbances (e.g. Pettit et al., 2021), but tree coring and laboratory analysis are time-consuming and thus costly. Lightning strikes creating scars in trunks are very rare stochastic events.	Fairly bad
	Tree density	LIDAR data	Using Bitterlich relascope or fixed-area plots	High for LIDAR; medium in the field	2 TreM groups potentially affected; the magnitude of expected effects is low to high, according to TreM types.	Evaluating tree density requires multiple measurements in the field since trees are not regularly distributed. However, data is often available as the recording of TreMs is usually done at the same time as the stand measurement.	Fairly bad
	Spatial distribution of the trees	LIDAR data	High precision GPS	High	1 TreM group potentially affected; the magnitude of expected effect is low.	Irrespective of the method used, recording accurate location of trees is always time-consuming and requires specific devices.	Bad
Tree	Bark feature	From literature, at	Irrelevant	Low	3 TreM groups potentially affected; the magnitude of	Literature search needs only to be done once.	Good

(continued on next page)

Table 3 (continued)

Grain	Feature	At the laboratory	In the field	Cost	Relevance for explaining the occurrence of TreM groups	Remarks	Trade-off
		the tree-species level			expected effects is low to high according to the TreM group.		
	Potential capacity to bear Mistletoe	From literature, at the tree-species level	Direct observation	Low	1 TreM group potentially affected; the magnitude of expected effect is high.	Mistletoe is actually a type of TreM and thus already routinely recorded.	Irrelevant
	Phyllotaxis	From literature, at the tree-species level	Irrelevant	Low	1 TreM group potentially affected; the magnitude of expected effect is low to high, according to the TreM type.	Literature search needs only to be done once.	Fairly good
	Proportion of heartwood vs sapwood	From literature, at the tree-species level	Irrelevant	Low	1 TreM group potentially affected; the magnitude of expected effect is low.	Literature search needs only to be done once. However, no data are available for most of the tree species.	Bad
	Architectural models	From literature, at the tree-species level	Irrelevant	Low	1 TreM group potentially affected; the magnitude of expected effect is low.	Only informative for young trees or for conifers that develop without changing their morphology (e.g. <i>Abies</i> spp., <i>Picea</i> spp., <i>Pseudotsuga menziesii</i>). Indeed, during their adult stage, most tree species duplicate their initial architectural pattern to build the main branches of the crown (Barthélémy and Caraglio, 2007). The architectural diversity of adult crowns is, therefore, much lower compared to that of young trees (Chomicki et al., 2017). Three main types of adult crowns can be distinguished: those of deciduous trees, those of conifers conforming to the initial pattern and those of the genus <i>Pinus</i> , which are intermediate between the two (Daina and Drénou, 2021).	Bad
	Compartmentalization capacity	From literature, at the tree-species or tree-genera level	Irrelevant	Low	1 TreM group potentially affected; the magnitude of expected effect is high.	Literature search needs only to be done once. Compartmentalization capacity is available for a few species only (see Oven and Torelli, 1999; Schneuwly-Bollschweiler and Schneuwly, 2012; Gilman, 2011; Dujesiefken and Liese, 2015).	Fairly good
	Physiological state	Remote sensing (Lambert et al., 2013)	Using the ARCHI method (Lebourgeois et al., 2015; Drénou et al., 2015)	Medium	4 TreM group potentially affected; the magnitude of expected effect is low to high according to TreM group.	Assessing physiological state would complement the results of studies that only compare snags and living trees. In the field, evaluating the physiological state of trees is challenging, since most methods are simply based on foliage discoloration and loss and do not take the resilience capacity of trees into account (Dujesiefken et al., 2005; Lambert et al., 2013). The ARCHI method (Lebourgeois et al., 2015; Drénou et al., 2015) is able to assess resilience capacity. However, it has to be developed for each tree species separately (Sabatier et al., 2014) and is currently available for only 15 species, including 7 broadleaves and 8 conifers (Joye, 2019). The observer needs to be able to assess the top part of the tree crown from a distance (Lambert et al., 2013) which can become challenging in dense stands and in difficult conditions, such as on	Fairly good

(continued on next page)

Table 3 (continued)

Grain	Feature	At the laboratory	In the field	Cost	Relevance for explaining the occurrence of TreM groups	Remarks	Trade-off
	Age	Irrelevant	By tree-coring	High	2 TreM groups potentially affected; the magnitude of expected effect is low to high, according to the TreM group.	steep slopes. Furthermore, few data are as yet available to assess the observer effect for the ARCHI status. Remote sensing methods require particular skills and are still under development. Tree-coring needs specific tools and materials, both in the field and at the laboratory. Furthermore, it needs skilled personnel to properly set a tree core. Tree-coring becomes especially challenging when the heartwood is already in an advanced stage of decay, which unfortunately occurs frequently in very large trees while these trees bear most of the TreMs.	Bad
	Ontogenic stage	Irrelevant	By counting the main forks	Medium	7 TreM groups potentially affected; the magnitude of expected effect is low to high, according to the TreM group.	Require prior training (Drénou et al., 2020).	Good

records.

Management intensity can also be evaluated using indices such as the Forest Management Intensity Index (ForMI, Kahl and Bauhus, 2014) or the Silvicultural Management Intensity Indicator (SMI, Schall and Ammer, 2013). These indices require additional information that can be challenging to assess post harvesting if you are not the local forest manager (e.g. the proportion of harvested tree volume for ForMI), or require reference data that are not always available (e.g. carrying capacity of a site in terms of basal area for SMI). Time since last harvest has been successfully used as a rough proxy for management intensity (Winter et al., 2015, Regnery et al., 2013b, Paillet et al., 2017), but does not account for a number of management practices that generate specific stand features after decades of set aside. Furthermore, it is important to keep in mind that the dynamics of TreM stock recovery are probably not linear over time (Larrieu et al., 2016; Paillet et al., 2019). Hence, time since last harvest should be modeled using time thresholds that are ecologically significant for determining key changes in TreM occurrence. The inaccuracy of time since the last harvest as a metric, lack of knowledge on the intensity of the last harvest, and our currently poor knowledge of the relevant thresholds for most forest types may explain why this factor had very low explanatory power for predicting TreM occurrence at the tree level in our dataset (Table 1). However, time since harvest does appear to have significant predictive power at the plot and stand scales (Paillet et al., 2017).

4.3. Trade-off between recording cost of additional features and their relevance for explaining the occurrence of TreMs

For practical issues, it is crucial to weigh the costs of recording an additional feature against its relevance for explaining the occurrence of TreMs. With the aim of selecting a sub-set of factors with the best compromise, we have summarised key elements for decision making in Table 3 for all the factors identified as potentially relevant.

4.4. Prioritization of additional site/stand/tree features that could be included in TreM databases

4.4.1. Acquisition of additional data from databases or in the field

Slope, exposure and altitude can be easily extracted from digital elevation models. However, recording these measurements in the field

does not take much time. Presence of cliffs can be evaluated from GIS. However, in the light of preliminary investigations performed in well-studied areas, we argue that it would be more useful to take field measures. Bark feature, phyllotaxis and compartmentalization capacity data need to be gathered from several sources which are available in the literature, and this needs to be done only once, at the tree-species level. However, compartmentalization capacity is currently available for only a few temperate tree species. To compensate for the lack of data at the tree species level, we assume that using data from a given species at the genus level could be an efficient and pertinent first step, while awaiting a more comprehensive assessment (see Larrieu et al., 2021).

4.4.2. Additional data that should be recorded in the field

Recording the ontogenic stage should be prioritised. To do this, observers must be well trained prior to fieldwork. For assessing the physiological state, the ARCHI method (Lebourgeois et al., 2015; Drénou et al., 2015) should be used if it is available for the dominant tree-species, keeping in mind that observers have to be properly trained to ensure high-quality data and to reduce the observer effect. In situations where trees are tall, stands are very dense or on steep slopes, employing the ARCHI method can become quite time consuming and one may refrain from recording this information. From our expertise, the additional sampling effort required to record these additional variables is estimated at five minutes per plot to check for cliffs and measure exposition and slope, plus five and three minutes per tree for the assessment of ARCHI status and ontogenic stage, respectively.

4.5. Expected value of this additional sampling effort and perspectives

This additional effort in terms of data acquisition could help promote the integration of TreM-related research into the applied field of biodiversity conservation. This would be particularly relevant for models of forest dynamics that include TreM occurrence in order to assess the mid- and long-term effectiveness of forest management strategies for TreM conservation. Work in this direction is ongoing, using for example the spatially explicit, individual-based forest dynamics model Samsara2 (Courbaud et al., 2015).

TreM conservation will continue to progress if forest managers perform routine assessments of TreMs in the field. To attain this goal, researchers have to identify the most relevant key factors to monitor,

while taking into account the extra effort required to add novel measurement protocols to current forest inventory practices. The effectiveness of management regimes in terms of TreM conservation will strongly depend on the motivation of the managers. This requires raising awareness and on-site training, combined with clear and applicable instructions, as well as a justifiable effort when selecting habitat trees. Most managers will be motivated to support such assessments if the above aspects are covered; other avenues may be to offer financial incentives, or by such data collection becoming a part of forest management planning.

5. Conclusion

Many environmental and tree-specific features that have rarely been considered until now by researchers studying TreMs appear to be promising candidates for improving the prediction of TreM occurrence and their dynamics. Several of these features can be easily measured in the field or extracted from large scale environmental databases. We suggest that future studies record a subset of nine features, in addition to variables already routinely recorded, to provide additional information to enable better prediction of the occurrence of particular TreMs: (i) at plot level: slope, exposure, altitude and presence of cliffs; and (ii) at tree level: bark feature, phyllotaxis and compartmentalization capacity of the tree species, plus ontogenic stage and physiological state of the tree sampled.

Author contribution statement

LL, BC and CD designed the general structure of the manuscript. MG run statistical analysis. RB, DKo, DKr, FK, TL, JM, YP, AS, JS, MS, KV contributed to discussion of the results and the writing of the final document.

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.

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Appendix A. Supplementary material

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.foreco.2022.120235>.

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