The Use of Tree-Related Microhabitats as Forest Biodiversity Indicators and to Guide Integrated Forest Management

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Abstract

Purpose of the Review The concept of tree-related microhabitats (TreMs) is an approach to assess and manage multi-taxon species richness in forest ecosystems. Owing to their provision of special habitat features, TreMs are of special interest as a surrogate biodiversity indicator. In particular, in retention forestry, TreMs have gained attention over the past decade as a selection criterion for retained structural elements such as habitat trees. This review seeks to (a) address the suitability of TreMs as biodiversity indicator in the context of retention forestry, (b) summarize drivers of TreM occurrence and the *status quo* of the implementation of TreM-based retention concepts in forest management, and (c) discuss current and future challenges to the use of TreMs as biodiversity indicator.

Recent Findings The TreM concept originated in Europe where it is now increasingly implemented. Most studies of the quantity, quality, and diversity of TreMs are focused on tree species from this region, although it is increasingly applied in other contexts. In addition to tree species, tree dimensions and live status have been identified as the main drivers of TreM occurrence. One major remaining research challenge is to verify relationships between the occurrence and abundance of forest-dwelling species from different taxonomic groups and TreMs to improve the evidence basis of this concept and thus increase its integration in forest conservation approaches.

Summary TreMs are not the “silver bullet” indicator to quantify biodiversity of forest dwelling species, but they provide an important tool for forest managers to guide the selection of habitat trees for the conservation of the associated biodiversity.

Keywords Retention forestry · Habitat trees · Sustainability indicator · Drivers of tree-related microhabitats

Introduction

Initial studies of tree-related microhabitats (TreMs) were conducted with individual typologies and definitions to capture the variation of microhabitats and to classify them according

to different habitat functions [1–3]. Nowadays, the most common definition for a tree-related microhabitat (TreM) is “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

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least a part of their life cycle to develop, feed, shelter or breed” [4••]. This definition was established during the course of an expert working group led by the European Forest Institute (EFI), which resulted in first recommendations for the application of a standardized TreM concept [5]. The hierarchical TreM typology for temperate and Mediterranean forests that was published by Larrieu et al. [4••] distinguishes 15 groups of TreMs in the following seven forms:

- Cavities: woodpecker breeding cavities, rot holes, concavities, insect galleries, and bore holes
- Tree injuries and exposed wood: exposed sapwood and/or exposed heartwood;
- Crown deadwood in different forms
- Excrescences: twig tangles (witches broom), cankers, and burrs
- Fruiting bodies of saproxylic fungi and slime molds: perennial and ephemeral fungi fruiting bodies
- Epiphytic, epixylic, and parasitic structures: epiphytic crypto- and phanerogams, nests of vertebrates and invertebrates, micro-soil (i.e. resulting from decay of lichens, mosses or leaf litter in either thick, old bark, or on horizontal limbs and forks for instance)
- Fresh exudates such as sap run and heavy resinosis

As reflected in the definition, the underlying concept is that TreMs represent a habitat component of different forest-dwelling species and thus they may indicate their potential presence. A variety of species from different taxonomic groups have been linked to the different TreMs used in the hierarchical typology. These include invertebrates such as insects, arachnids, and gastropods as well as vertebrates such as birds, rodents, bats, and carnivores [4••].

Most information on TreMs stems from literature that originated in the context of retention forestry [6, 7]. Retention forestry belongs to a set of integrative biodiversity conservation strategies [8] and focuses on the provisioning of particular, biodiversity-relevant, often old-growth structures that are otherwise lacking or reduced in forests managed for wood production [9, 10]. These structures are supposed to provide a life-boating function for the associated species or act as stepping stones between larger retention patches, forest reserves, or primary forest remnants and thus increase the connectivity in managed forests [11, 12] and even the full habitat for a viable population for very specific taxonomic groups. Apart from coarse woody debris, living and standing dead trees have been central to most of these retention concepts within Europe and elsewhere [13, 14]. These elements are mostly referred to as habitat trees (or veteran, senescent, or wildlife trees). Habitat trees are broadly defined as large, old, living, or dead microhabitat-bearing trees that are or could become more important to biodiversity than the average tree in a managed forest [15]. The idea of habitat tree conservation

has a long tradition in temperate European forests [16], but in earlier times, it was not as systematically applied as is the case now under integrative approaches in forest management such as retention forestry [13••]. TreMs are of special interest in continuous-cover forestry, where they are used as criteria to select habitat trees for retention [13, 17]. While TreMs have so far been used mostly in this context, they can equally well be used in other types of forest management as well as the management of urban parks and street trees [18]. In addition, they are useful for communication of biodiversity focused forest management approaches [19]. Against this background, this review seeks to:

- Address the function of TreMs as biodiversity indicators in the context of integrative forest management approaches such as retention forestry
- Synthesize drivers of TreM occurrence and the *status quo* of implementations of TreM concepts in forest management
- Discuss current and future challenges of TreMs as biodiversity indicators

The Potential of TreMs as Biodiversity Indicators

There is a large and growing body of literature on different types of indicators of forest biodiversity [20–26]. Various attempts have been made to develop indicators of forest biodiversity for large gradients of spatial and temporal scales. These range from the use of single keystone or flagship species to faunal [27] or structural surrogates (e.g., deadwood [22, 28]). An indicator is a measure of a quantity or a phenomenon that is easier to assess than its target (viz., the *indicandum*). The use of an indicator should also bring more information than the raw measure of the *indicandum* only. The validation of biodiversity (or environmental) indicators in ecological studies strongly focuses on the correlation between the indicator and its *indicandum*: for a given indicator to be validated, the correlation with its *indicandum* should be strong and significant [29]. However, the thresholds for a correlation to be considered “strong” for this purpose are rarely defined, while statistical significance mostly depends on the sample size analyzed. Therefore, it seems that this validation process should rely on a wider set of criteria, as commonly applied in political and human sciences [30]. From the broader point of view of social sciences, and particularly of political sciences, indicators are frontier objects that allow communication between science, policy, and society, and the assessment of their usefulness should be based on many more criteria than only the correlation with the *indicandum* [31•]. While correlation and causality rely on ecological theory, mostly on different conceptual approaches of the relationship between species and their habitat

(e.g., niche theory, habitat amount and heterogeneity hypotheses [32]), broader views of indicator usefulness include social acceptance, policy relevance, and comprehensibility (see Table 1 in [30] for an overview).

The Organization for Economic Co-operation and Development (OECD), which has a long history of developing and using environmental indicators for reporting purposes, suggests that “indicators should be assessed/evaluated according to their (i) policy relevance, (ii) analytical soundness, and (iii) measurability. The [...] ideal indicator for measuring progress should be [...] policy-relevant and meaningful, biodiversity relevant, scientifically sound, accepted by a broad public, lend itself to affordable monitoring and modelling, and be sensitive enough to detect changes in systems within timeframes and on scales relevant to decision-making” [31]. Indicators are similarly defined in the criteria and indicator processes that have been initiated to support sustainable forest management around the globe since the United Nations Conference on Environment and Development (UNCED) of Rio 1992 (e.g. [33]). In this regard, one might ask whether TreMs, when used as biodiversity indicator, meet these criteria proposed by the OECD [31]. Among others, the Pressure-State-Response (PSR) framework used by the OECD has received some attention in forest and biodiversity science to address various types of questions [21, 34, 35]. The PSR framework has been developed to provide information to respective users in a causal way by differentiating between causes (pressure) of changes in biodiversity, effects on biodiversity (state) caused by the specific pressure, and societal responses to assess and remedy the human impacts on nature [35]. As mentioned above, there are other frameworks than the PSR that use biodiversity indicators for sustainability assessments. However the PSR framework exemplifies the relevance of TreMs as indicators of the state of forest biodiversity. In the context of integrative nature conservation practices such as retention forestry, TreMs could be used as meaningful structural indicators for the state of biodiversity at the stand scale. In this context, one major **pressure** on biodiversity in forests may be expressed as the proportion of forest biomass productivity that is appropriated (harvested) for human consumption [36, 37]. The harvesting of forest biomass is associated with the direct loss of habitats and the removal of energy and nutrients to develop extensive food chains/networks, which halts the development of old-growth habitat. Related to this pressure, TreMs could indicate the **state** of the diversity of forest dwelling species by describing the *status quo* of the provisioning of suitable habitats in managed and unmanaged forests [17, 38–40]. TreMs could be used to quantify the biodiversity at a structural, indirect level [41, 42]. It has been shown that TreMs are sensitive to the above pressure with lower abundance and diversity in managed than in medium- or long-term unmanaged forests. TreMs could be a useful and convenient indicator because their assessment, like that of

dead wood, could be readily integrated into many types of terrestrial forest inventories, ranging in scale from the ownership to the national level (e.g., [28, 43]). For example, in forest inventories that already quantify the number of habitat trees, it would be a logical next step to quantify TreMs (e.g., [13•]). Since there is, owing to the very high costs that would be involved, no routine inventory of a wide range of forest-dwelling species across the forest landscape, the indirect indication of potential habitat could provide this information efficiently across forest types, ownerships, etc. A related societal **response** to this pressure and an undesired state in the provision of habitats could be indicated by the proportion of forestland that is in strict reserves or managed with a retention forestry approach, which is already required in different certification systems [13, 44]. Retention forestry aiming at maintaining forest organisms, structures, and connectivity to support biodiversity and ecosystem functioning beyond harvesting interventions would be closely related to the above pressure and state indicators. Following an adaptive management concept, TreMs could then offer a way to quantify habitats provided by retention forestry and thus assess the success of the retention forestry approach.

In addition to the mentioned PSR framework, in an earlier meta-analysis on types of biodiversity indicators, TreMs were classified as “temporal and other structural indicators” which are especially relevant at the stand scale [20]. Temporal indicators refer to indicators that are able to quantify shifts in the state of the biodiversity in a specific ecosystem over time. With regard to international sustainable forest management processes such as Forest Europe, TreMs could potentially be used as an indicator for the criterion biodiversity, where currently “Deadwood” and “Naturalness”, among others, already serve as quantitative indicators [45]. To be used as biodiversity indicator in these international processes that promote sustainable forest management, TreMs would have to be routinely quantified in national forest inventories of the participating countries.

In contrast to quantifying the occurrence or abundance of single or multiple species, which are difficult and/or expensive to assess at the stand scale, TreMs offer an applicable indicator of biodiversity at the stand scale. In the context of measurability, cost is an important property, which is relatively low compared with more labor and time-consuming inventories of a wide range of different species that are additionally often bound to specific times (e.g., breeding/non-breeding season) of the year. This does not necessarily hold true for all species groups, but certainly regarding the multi-taxon level information that TreM inventories provide. TreM inventories can be carried out throughout every season, although leafless and snow-free periods are preferred. This could especially be relevant, when TreM inventories are included in already existing forest inventories. This applicability is an important aspect for a forest biodiversity indicator. An illustration of the lack of

Table 1 Examples of the use of tree-related microhabitats (TreMs) as selection criteria for retention elements in managed forests as stated in management concepts of publicly owned forests at regional and national

levels in four countries of Central Europe as well as certification schemes for Germany

TreM typology following Larrieu et al. [4]			Regional level														National level			
			GER ¹														CH ²	GER ³	AT ⁴	FR ⁵
Form	Group	TreM	BB	BW	BA	HE	MV	LS	NW	RP	SH	SL	SN	ST	TH	GR	PEFC	FSC	ÖBF	ONF
Cavities	Woodpecker breeding cavities	Small cavity	✓	✓	✓	✓	✓	✓	✓	✓	✓	✓	✓	✓	✓	✓	✓	✓	✓	✓
		Medium-sized cavity	✓	✓	✓	✓	✓	✓	✓	✓	✓	✓	✓	✓	✓	✓	✓	✓	✓	✓
		Large cavity	✓	✓	✓	✓	✓	✓	✓	✓	✓	✓	✓	✓	✓	✓	✓	✓	✓	✓
		"Flute" (cavity string)	✓	✓	✓	✓	✓	✓	✓	✓	✓	✓	✓	✓	✓	✓	✓	✓	✓	✓
	Rot holes	Trunk base rot hole		✓	✓	✓	✓	✓	✓	✓	✓	✓	✓	✓	✓	✓	✓	✓		✓
		Trunk rot hole		✓	✓	✓	✓	✓	✓	✓	✓	✓	✓	✓	✓	✓	✓	✓		✓
		Semi-open trunk rot hole													✓	✓	✓	✓		
		Chimney trunk base rot hole			✓	✓	✓	✓	✓	✓	✓	✓	✓	✓	✓	✓	✓	✓		✓
		Chimney trunk rot hole		✓	✓	✓	✓	✓	✓	✓	✓	✓	✓	✓	✓	✓	✓	✓		✓
		Hollow branch				✓	✓	✓	✓	✓	✓	✓	✓	✓	✓	✓	✓	✓		
Tree injuries and exposed wood	Insect galleries and bore holes	Insect galleries and bore holes		✓												✓				
	Concavities	Water-filled holes														✓				
		Woodpecker foraging excavation														✓				
		Trunk bark-lined concavity														✓				
		Root buttress concavity														✓				
	Exposed sapwood only	Bark loss		✓		✓	✓		✓	✓		✓	✓	✓	✓	✓				
		Fire scar														✓				
		Bark shelter		✓						✓					✓	✓				
		Bark pocket		✓						✓					✓	✓				
		Stem breakage	✓	✓	✓	✓			✓	✓		✓	✓	✓	✓	✓				
		Limb breakage	✓	✓					✓	✓				✓	✓	✓				
		Crack	✓	✓		✓	✓					✓	✓	✓	✓	✓				✓
		Lightning scar	✓			✓			✓	✓		✓	✓	✓	✓	✓				
		Fork split				✓								✓	✓	✓				
Crown dead-wood	Crown dead-wood	Dead branches		✓											✓	✓				
		Dead top		✓						✓		✓			✓	✓				
		Remaining broken limb													✓	✓				
Excrecences	Twig tangles	Witches broom														✓				
		Epicormic shoots														✓				
	Burs and cankers	Burr		✓			✓								✓	✓				
		(Decayed) Canker		✓			✓				✓				✓	✓				
Fruiting bodies of saproxylic fungi and slime molds	Perennial fungal fruiting bodies	Perennial polypore		✓						re S	✓	✓	✓	✓	✓	✓				
		Annual polypore									✓	✓	✓	✓	✓	✓				
	Ephemeral fungal fruiting bodies and slime molds	Pulpy agaric														✓				
		Pyrenomycete														✓				
		Myxomycete														✓				
Epiphytic, epixylic and parasitic structures	Epiphytic or parasitic crypto- and phanerogams	Bryophytes		✓					✓	✓						✓				
		Lichens		✓					✓	✓						✓				
		Ivy and lianas		✓					✓	✓						✓				✓
		Ferns														✓				✓
		Mistletoes														✓				✓
	Nests	Vertebrate	✓	✓	✓	✓	✓	✓	✓	✓	✓	✓	✓	✓	✓	✓	✓	✓		✓
		Invertebrate														✓				
	Micro soils	Bark														✓				
		Crown														✓				
Fresh exudates	Fresh exudates	Sap run		✓								✓				✓				
		Heavy resinosis														✓				

Light gray indicates a consideration at the level of TreM form, dark gray refers to TreMgroups and, ✓ " indicates the mentioning of the specific TreM in the concept following the typology of Larrieu et al. [4]. White or empty cells indicate no consideration of TreMs in the respective concept.

¹ GER = Germany; BB = Federal state (FS) Brandenburg; BW = FS Baden-Württemberg; BA = FS Bavaria, HE = FS Hesse; MV = FS Mecklenburg-Vorpommern; LS = FS Lower Saxony; NW = FS North Rhine-Westphalia; RP = FS Rhineland-Palatinate; SH = FS Schleswig-Holstein; SL = FS Saarland; SN = FS Saxony; ST = FS Saxony-Anhalt; TH = FS Thuringia; ² CH = Switzerland; GR = Canton Graubünden; ³ PEFC = Program for the Endorsement of Forest Certification Schemes; FSC = Forest stewardship council; ⁴ AT = Austria; ÖBF = Austrian national forest service; ⁵ FR = France; ONF = French national forest service. For specific references to the mentioned guidelines see SI

measurability of other indicators at the stand scale are certain insect indicator species, which often have much finer requirements on spatial scales [46, 47] compared, for instance, with indicator species of birds [23] that require usually larger sampling areas. Therefore, inventories of TreMs, and more generally structural attributes, offer an interesting complementary alternative.

Determinants of Tree-Related Microhabitat Occurrence

TreMs, in varying forms and definitions, have been investigated in forests for more than a decade, and we now have an increasingly sound knowledge basis that can be synthesized [1, 3, 18, 48]. The underlying importance of analyzing driving factors of TreM occurrence was pointed out in the definition by the OECD, which states that indicators should be scientifically sound and sufficiently sensitive to detect changes between systems at relevant scales [31•]. Therefore, understanding drivers of this potential biodiversity indicator delivers the basis to assess its usefulness and to identify contexts in which TreMs could be a valuable tool. The research on TreMs has had a strong regional focus in Central-Europe and the Mediterranean, notably the typology of TreMs [1, 3, 17, 39, 48–50]. Therefore, most of the studies are related to TreMs on tree species that occur in these regions, mostly European beech (*Fagus sylvatica* L.), silver fir (*Abies alba* Mill.), Norway Spruce (*Picea abies* L.), as well as different European oak species (*Quercus* spp.) [1–3, 17, 49, 51]. There are fewer studies on tree species such as Douglas fir (*Pseudotsuga menziesii* (Mirb.) Franco) or Oriental beech (*Fagus orientalis* Lipsky (Fo)) from outside Europe [52–56]. All these studies have in common that tree species is a determining factor of TreM abundance and richness. Commonly broadleaf trees or forest types that include shares of broadleaves provide more TreMs than coniferous ones [17, 49].

A second important determinant of TreM occurrence is tree dimension. In this regard, diameter at breast height (DBH) has proven to be a strong and significant driver of TreM occurrence in all studies that considered this common mensurational variable [e.g., 15, 34, 39]. In general, large trees support a greater abundance and richness of TreMs across all tree species [51, 52, 57, 58]. It is not fully understood whether tree species or dimension is more decisive, but both are usually the two most important drivers of TreM occurrence. It should be noted that there are, to the best of our knowledge, so far just one modeling study [59] and one study based on observational data [60] which have made the effort to analyze the relationship between tree age and TreMs. Other studies understood tree dimension as an indirect measure of tree age [17•], although this relationship between diameter and age can be extremely variable, in particular in uneven-aged forests (e.g., [61]). Tree

dimension is also related to the crown position class of trees, typically declining from dominant, to co-dominant, intermediate, and suppressed trees. This crown position class might have some effect on TreMs as well, since trees of different crown classes have undergone divergent developments and are exposed to different processes with relevance to TreM formation; e.g., wind breakage of large limbs might be greater in trees in the top canopy layer [62]. There have been only a few studies that have considered crown class, but it seems that mostly large, dominant trees in the upper canopy layer provide more TreMs than suppressed ones [58]. The relatively recent establishment of the TreM concept as well as the time required for trees to form TreMs did not allow the establishment of reliable time series based on longitudinal observations of their development on the same trees at this stage.

The third major determinant of TreMs is the live status of trees [49, 51, 58]. In most cases, standing dead trees or snags provide more TreMs than living trees of comparable dimensions [49, 57]. For instance, the TreM groups of woodpecker feeding holes as well as saproxylic fungi have been found more frequently on snags [49, 51].

Lastly, the frequently assessed influence of forest management has been considered a crucial determinant for the occurrence of TreMs [17, 39, 53, 57]. However, the relationship of management types and TreM richness is not trivial to scrutinize. The management influence varies with the silvicultural systems applied, as harvesting might on the one side remove habitat trees and on the other side damage trees and thus trigger the developments of new TreMs such as exposed heart wood or broken limbs. In central Europe, for instance, continuous cover forestry, and more particularly close-to-nature forest management, is often practiced [63, 64]. In this approach a selection of habitat trees with a focus on small structures such as TreMs throughout the whole landscape is feasible at small spatial scales, whereas in even-aged forestry with larger management units, this is likely more difficult [13, 65]. Owing to the different retention approaches in forest management, such as simply maintaining certain basal areas or volumes as practiced in other parts of the world, for instance, in Canada [53•], clear patterns of TreMs in response to management are difficult to establish. In remnants of clearcuts, TreMs were almost absent, whereas shelterwood treatments maintained TreM numbers similar to uncut control plots in mixed hardwoods [53•]. In Europe, in contrast, there were no differences in TreMs between uneven-aged and even-aged stands of the same forest type [17•], whereas other factors such as the time since last harvest and the difference in number of snags between managed and unmanaged stands were more important [57]. In addition, there is so far little information from old-growth or primary forests to facilitate comparisons with managed forests. However two studies have provided first reference numbers of TreMs for primary forests of European beech and Oriental beech [38, 52].

Implementation of Tree-Related Microhabitats as Biodiversity Indicators

The relevance of TreMs as biodiversity indicators is underpinned by the fact that the TreM concept has been widely adopted in integrative conservation concepts in temperate forests of central Europe. For example, a number of institutions, federal states, as well as certification schemes (PEFC, FSC) in Germany, Austria, Switzerland, and France use TreMs as selection criteria for habitat trees (Table 1; [66]), although they often are referred to with other terms. When compiling information for Table 1, we did not attempt to provide a full coverage of locally implemented concepts, but included recommendations that were implemented at least at a regional level (Table 1). In addition to guidelines implemented at regional levels (e.g., federal states in Germany), national certification standards suggest the use of TreMs for the selection of retention elements (Table 1). The integrative conservation concepts listed here evolved from the need for a systematic and precautionary consideration of legally protected habitats in forest management, which include large vertebrate nests or woodpecker cavities [67, 68]. These concepts might as well include microhabitats that are essential for other organisms (mainly invertebrates) [4••]. Most recommendations are valid for state forests, and in some cases other public forests, but do not necessarily apply to private forests. These concepts often focus on TreM groups or single TreMs as guidance for forest managers to indicate trees that have a higher than average natural value and may be set-aside for retention purposes (Table 1). If a certain tree bears a TreM that is recognized as a (legally) protected microhabitat, it has to be retained as habitat tree. TreM-bearing trees can be set aside individually [65] or in the form of small retention patches, so called habitat tree groups or set-aside islands. Besides woodpecker cavities, rot holes, and large vertebrate nests, which are a mandatory selection criteria in all of the mentioned guidelines, injuries exposing sap- or heartwood as well as fruiting bodies of saproxylic fungi are frequently considered as TreMs as well, to qualify individuals as habitat trees (Table 1). Crown deadwood and excrescences, such as burrs and canker or exudates, are rarely listed as criteria for selecting habitat trees. However, more recently approved or updated management guidelines consider a broader range or the full spectrum of the current TreM typology (e.g., in the German state of Baden-Württemberg or the Swiss canton Graubünden; Table 1). In addition to the presence of TreMs, trees are commonly selected for retention based on exceptional dimensions or bizarre shapes (Table SI 1). Also tree species is often an important selection criterion when the aim is to conserve rare tree species or those with high species-specific dependent biodiversity [40]. Most commonly, the retention concepts are applied in older forest stands entering the harvesting phase and aim at maintaining five to ten habitat trees per hectare. Formerly used, partly anecdotic, descriptors to identify habitat trees referring to “ancient

trees,” “senescent trees,” or “veteran trees” are becoming more commonly objectively described with the help of the TreM typology.

Current and Future Challenges of Tree-Related Microhabitats as Biodiversity Indicators

From an ecological point of view of, the validation of TreMs as biodiversity indicators crucially relies on the improvement of our understanding of their link with actual species diversity and abundance. While numerous studies (listed in [4, 69]) have empirically established the dependence of some species and groups to certain microhabitat types, they usually do so without a quantification of the link, frequently lacking evidence for the actual strength of the relationship. In addition, most of the correlations between the occurrence of certain species, species richness, or diversity and microhabitat metrics recently observed remain relatively noisy and are moderately associated [41, 42, 48, 70]. Such relationships with overall richness or specific types of TreMs based on observational studies at the stand (plot) level have been reported so far for birds, bats, and to a lesser extent (saproxylic) insects [41, 42]. The noise in these relationships is partially caused by the fact that forest-dwelling species included do not directly rely on any of the inventoried TreMs for their habitat requirements or the habitat range does not match the spatial scale at which TreMs have been inventoried. For example, some studies have ignored TreMs on dead wood [17, 52]. This could have a significant impact on the result as not all species rely exclusively on TreMs borne by living trees and more TreMs occur on snags compared with living trees [57]. Still, such relatively low levels of correlation are not uncommon to other popular structural biodiversity indicators such as deadwood [22]. Other variations in biodiversity that structural indicators can typically not capture is the spatial and temporal context that strongly influences species richness of the associated taxa; this includes site conditions such as climate or distance to source populations as well as management history [12, 64].

These results of the correlations between TreMs and species either concern indices based on microhabitat lists (such as microhabitat diversity [41••]) or individual microhabitats (e.g., conks of fungi and cavities [70]), but they all have in common observational methods at the stand (plot) scale that do not target specific TreMs. Such methods have the advantage of covering a large range of TreM types and taxonomic groups and, in the latter case, are reputed to correctly assess the stand or plot-related richness at community level (e.g., window traps for beetles [71], point counts for birds [23]). However, the cumulative effects of detection errors for both TreMs [72] and the associated taxonomic groups, and more generally the difficulties to approximate true abundance

levels, may partly explain the noise in correlations, next to the spatial-temporal factors. In addition, sampling species diversity at a plot level may overlook species specific to certain TreMs, especially smaller invertebrates or rare species [73]. Such sampling methods are also limited for assessing robust causal and functional links between specific microhabitats and species richness of the assessed taxonomic groups, but are a crucial step in the validation of TreMs as an indicator of overall species richness.

Some ways to improve TreM inventories have been suggested [4, 72, 74], for instance conducting inventories with standardized recording protocols and teams of more than one observer, yet their efficiency has not been tested rigorously. To monitor or prevent observer bias, repeated measurements or comparative studies of TreMs with standardized protocols and the same teams would be necessary [72]. Other approaches have focused on the use of remote sensing techniques to identify TreMs either at the tree-level directly [74, 75] or to predict the occurrence of trees bearing TreMs from stand characteristics [76•] both from terrestrial laser scanning as well as airborne inventories. However, to detect the full range of TreMs from these inventories or to predict the location of habitat trees accurately for forest management remains a future challenge.

Similarly, a first step towards the improvement of standardized sampling of taxonomic groups would be to combine different sampling methods targeting taxa directly at the microhabitat level rather than relying on correlational studies. For example, some studies correlating microhabitat indices with saproxylic beetle diversity used only interception traps [71, 77]. A broader view of the saproxylic insect community as well as better estimates of abundance in direct relation to TreMs could be obtained through the combined use of different sampling methods such as pitfall traps, interception traps, and malaise tents at the entrance of cavities, for instance [e.g., 70]. Another approach would be targeted sampling of specific species or their DNA in relation in specific types of TreMs (e.g., [78]). For particular groups of vertebrates, the combination of automatic acoustic methods, camera traps, and classical point counts may lead to better community estimates [79]. Finally, relatively new approaches involving genetic methods as environmental DNA metabarcoding and bulk sample metabarcoding have been shown to provide an overview of species using specific TreMs (e.g., [80]).

Another way to improve knowledge on microhabitat-dwelling species and specifically infer causal (functional) links would be to build controlled experimental designs involving artificial microhabitats. Most examples in the literature involve artificial cavities for birds [81, 82], but also for beetles [83], as well as other “easily” created microhabitats such as dendrotelms (water-filled holes [84]). Such experimental approaches provide a high level of evidence for species-TreM relationships, but their set-up is limited to TreMs that can be artificially created. In addition, an experimental approach involving a controlled set of TreMs is far more difficult than observational studies—if even

possible—to set up, because the way TreMs are created is highly variable and not necessarily reproducible. In this sense, complementary approaches using both observational and experimental methods appear to be most promising. This work is ideally shared within large, international networks involving forest managers and ecologists working at different scales and with different perspectives [85].

Ways to Validate Tree-Related Microhabitats as Biodiversity Indicators beyond Species Inventories

Ecological sciences consider the correlation between indicator and *indicandum* as the main criterion of validation [30, 86]. The use of TreMs as biodiversity indicators is no exception to this rule, and while so far relatively weak statistical correlations with different taxonomic groups have been documented, TreMs have been widely accepted by forest managers and the wider public as a tool to promote and assess integrative, conservation-minded forest management (see Table 1, [4, 5]). In addition, TreMs allow and accelerate communication between different stakeholders with various backgrounds [87•] which is important to reduce forest degradation as pointed out for deadwood [88]. In this sense, the interest of TreMs as a communication and education tool to forest biodiversity conservation is considerable and should be taken into account when assessing their usefulness as biodiversity indicator. This is in line with the criteria stated by the OECD that ideal biodiversity indicators should also be policy-relevant and accepted by the broad public [31•]. However, care must be taken that these aspects do not become more important than the relationship between indicator and *indicandum*. The remaining challenge is therefore to combine the evidence on ecological functions of TreMs with policy and management utility to fully assess the role of TreMs as biodiversity indicators.

Conclusions

TreMs are not the “silver bullet” indicator to quantify and predict species richness. Nevertheless, through their relationships with species from many taxonomic groups [41, 42], they have the potential to indicate habitat quality for a large section of forest-dwelling species, often better than other established indicators such as single focal species or red-list species [24, 27]. Combined with other types of direct or indirect (e.g., structural) biodiversity indicators, standard TreM inventories have the potential to capture a large proportion of forest biodiversity.

TreM inventories are tailored at the stand scale, making them relevant and readily implemented in forest management. In addition, TreMs are broadly recognizable and intelligible to the broad public, and constitute tangible tools for communication of conservation efforts in forests. Therefore, TreMs already provide an applied and implemented approach for forest managers for the conservation of forest biodiversity through the retention of habitat trees. Further studies, especially outside Europe, are now needed to assess their indicative power and conservation relevance.

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Compliance with Ethical Standards

Conflict of Interest There are no conflicts of interests to declare.

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