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Tree related microhabitats in temperate and Mediterranean European forests: A hierarchical typology for inventory standardization

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ABSTRACT

Tree **re**lated **M**icrohabitats (hereafter TreMs) have been widely recognized as important substrates and structures for biodiversity in both commercial and protected forests and are receiving increasing attention in management, conservation and research. How to record TreMs in forest inventories is a question of recent interest since TreMs represent potential indirect indicators for the specialized species that use them as substrates or habitat at least for a part of their life-cycle. However, there is a wide range of differing interpretations as to what exactly constitutes a TreM and what specific features should be surveyed in the field.

In an attempt to harmonize future TreM inventories, we propose a definition and a typology of TreM types borne by living and dead standing trees in temperate and Mediterranean forests in Europe. Our aim is to provide users with definitions which make unequivocal TreM determination possible. Our typology is structured around seven basic forms according to morphological characteristics and biodiversity relevance: i) cavities *lato sensu,* ii) tree injuries and exposed wood, iii) crown deadwood, iv) excrescences, v) fruiting bodies of saproxylic fungi and fungi-like organisms, vi) epiphytic and epixylic structures, and vii) exudates. The typology is then further detailed into 15 groups and 47 types with a hierarchical structure allowing the typology to be used for different purposes. The typology, along with guidelines for standardized recording we propose, is an unprecedented reference tool to make data on TreMs comparable across different regions, forest types and tree species, and should greatly improve the reliability of TreM monitoring. It provides the basis for compiling these data and may help to improve the reliability of reporting and evaluation of the conservation value of forests. Finally, our work emphasizes the need for further research on TreMs to better understand their dynamics and their link with biodiversity in order to more fully integrate TreM monitoring into forest management.

1. Introduction

Over the last decades, biodiversity conservation has become an increasingly important management objective in multi-purpose forests (Hunter, 1999; Kraus and Krumm, 2013). However, despite large-scale forest initiatives (Convention on Biological Diversity, 1992; European Environmental Agency, 2008; Forest Europe, 2015), monitoring forest biodiversity or structural heterogeneity remains a challenge

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(Lindenmayer et al., 2006). In conventional forest inventories, direct biodiversity monitoring is often limited to only one, or a few, species groups because reliable records of biota are expensive and time-consuming and require taxonomic experts for inventory and interpretation (Winter et al., 2008). In addition, no taxon has been firmly identified as a relevant surrogate for all the other taxa yet (Wolters et al., 2006). Since total biodiversity cannot be measured due to its complexity, indirect methods have been developed, especially for species diversity (Larsson, 2001; Lindenmayer et al., 2000). Both management and nature conservation in forests focus mainly on general forest structure characteristics that are assumed to be essential for biodiversity and that can be influenced by forest management (Chirici et al., 2012; Winter et al., 2014). These characteristics include horizontal and vertical forest structure, tree species composition, tree age, tree diameter distribution, tree regeneration, and deadwood quantities and qualities. Efforts to include structurally based biodiversity indicators have notably relied on National Forest Inventory data (Food and Agriculture Organization, 2015; Forest Europe, 2015).

Emphasis has been put on biodiversity-related structures such as deadwood (e.g. Stokland et al., 2012) for which thresholds (Müller and Bütler, 2010) and references have been published (e.g. Christensen et al., 2005; Paillet et al., 2015b; Vandekerkhove et al., 2009). For example, deadwood volume has been used as a structural indicator for forest biodiversity monitoring in most European forest inventory protocols during the last two decades (Tomppo et al., 2010). Clear definitions and survey methods for assessing deadwood allow comparative studies (e.g. Christensen et al., 2005; Vandekerkhove et al., 2009), inventories and analyses to be carried out in a harmonized way (Rondeux et al., 2012).

In the quest for scientifically-based indirect structure indicators (Larsson, 2001), tree related microhabitats (hereafter refered to as TreMs) have recently gained attention in research and management (e.g. Larrieu and Cabanettes, 2012; Michel and Winter, 2009; Regnery et al., 2013b; Siitonen, 2012; Vuidot et al., 2011; Winter et al., 2015b; Winter and Möller, 2008). Many studies focus on individual types, mainly cavities (e.g. Carvalho et al., 2014; Gouix and Brustel, 2012; Ranius et al., 2009; Remm and Lõhmus, 2011; Saunders et al., 2014). Among the authors who have studied several TreM types simultaneously (e.g. Kraus et al., 2016; Larrieu and Cabanettes, 2012; Larrieu et al., 2014a; Michel and Winter, 2009; Paillet et al., 2017; Vuidot et al., 2011; Winter and Möller, 2008), the definitions and lists used and the observation protocols applied generally differ. There are considerable variations among interpretations of what exactly a TreM is and which features should be recorded in the field. As a consequence, the results from different studies are hardly comparable, despite the harmonizing efforts of Larrieu et al. (2014b) and Winter et al. (2015b). Clear definitions as well as a standardized list and methodology are now needed to make it possible to compare studies focusing on the role of TreMs for biodiversity at the stand scale and to promote TreMs as biodiversity indicators in large-scale monitoring efforts.

Our first aim is to provide a clear definition of a TreM. Secondly, we propose a TreM typology with strong morphological and biodiversity relevance. Thanks to the hierarchical structure of our typology, it can be used by both researchers and forest managers; for example, as a tool to identify and conserve habitat trees in managed forests. We also provide guidelines for recording methods and required measurements to serve as a baseline for common application in monitoring, research and teaching. Finally, we discuss the relevance of the proposed typology and propose research perspectives in order to fill in the gaps in the current knowledge of TreMs. In particular, we emphasize the need to better understand TreM dynamics, relative to the specific forest context, and the link between specific TreMs and biodiversity.

2. Tree related microhabitats: a definition based on their functional role for biodiversity

2.1. *Definition*

We define a Tree related Microhabitat (TreM) as a distinct, well delineated structure occurring on living or standing dead trees, that constitutes a particular and essential substrates or life site for species or species communities during at least a part of their life cycle to develop, feed, shelter or breed. TreMs are specific above-ground tree morphological singularities that are not to be found on every tree. TreMs encompass both tree-originating modifications caused by biotic and abiotic impacts, such as intrusions, lesions and breakages, which expose sap and heartwood and initialize outgrowth structures and wood decay (saproxylic TreM), as well as elements of external origin that are physically linked to the tree (epixylic TreM).

Although morphological singularities may also be observed on lying deadwood or roots, TreM are explicitly restricted to above-ground structures on standing trees, in order to avoid a too wide scope. Thus, we have deliberately excluded features of lying deadwood such as root plates, pits and mounds and particular wood decay structures. We also exclude generic tree species-specific characteristics, such as rough bark on oak or larch, acid or alkaline bark conditions, as well as peculiar tree growth forms (such as crooked, skewed or rotated trunks, low horizontal branching), resulting from specific abiotic conditions or haphazard growth.

2.2. *Substrates and microclimates associated with TreMs*

TreMs provide specific conditions, notably microclimatic conditions and substrates, where specialized taxa shelter, forage or breed. Therefore, there is a functional link between TreMs and species, ecological groups or guilds. In other words, TreMs constitute very small-scale habitat (or part of habitat) for associated and specialized species or species assemblages. TreMs thereby strongly contribute to the internal heterogeneity of forest stands. We classified the TreMs into 15 main microhabitat groups according to 12 substrates and four microclimatic conditions they provide (Table 1). The rarest substrates occurring in our typology are charred wood (from fire or lightning injuries), hyphal structures (on fungi conks), epixylic materials and supporting structures (such as nests). Other substrates are more common (e.g. exposed sap- and heartwood). Twelve out of fifteen TreMs supply buffered microclimates (mainly cavities) while one provides temporary water bodies (dendrotelm). Eight TreM groups provide potentially drier conditions than the surrounding microclimate, while seven TreM groups support higher humidity. Some TreMs, such as rot-holes, can offer either dry or wet microclimatic conditions depending on the time of the year: during rainy periods, such cavities offer a dry shelter, whereas during dry periods they still offer a relatively moist habitat.

2.3. *Biodiversity associated with TreMs*

TreMs are patchy substrates that evolve constantly; they can therefore be considered as “ephemeral resource patches” (as defined by Finn, 2001). They are used by a wide variety of animals, plants and fungi, during at least a part of their life-cycle. Based on the literature (Appendix A) and the authors’ expertise, we have selected nine broad taxonomic groups which use TreMs: insects, arachnids, gastropods, birds, mammals, amphibians and reptiles, bryophytes, fungi, lichens (Table 2). This supporting information does not aim to be exhaustive, but illustrates both the diversity and specificity of TreM-dwelling assemblages, some species being exclusively linked to certain TreM types (see e.g. Dajoz, 2007 for dendrotelm-dwelling species).

Arthropods are by far the main known users of TreMs with a large range of taxa concerned (see e.g. Dajoz, 2007; Stokland et al., 2012).

Table 1
Substrate types and microclimatic conditions associated with specific tree-related microhabitat (TreM) groups in European temperate and Mediterranean forests. X: feature systematically exhibited; (X): feature not systematically exhibited; [a]Mould consists of decayed wood commonly mixed with animal detritus; [b]Soil humus mixes organic and mineral components; [c]Organic humus consists of leaves, twigs, bryophytes, detritus, etc.; [d]Supporting structure is additional tree biomass not originating from regular tree growth.

TreM Groups	Substrate type											Supporting structure[d]	Microclimatic conditions			
	Sapwood	Heartwood	Mould[a]	Soil humus[b]	Organic humus[c]	Animal detritus	Sap	Resin	Epixylic material	Hyphal structure	Charred wood		Buffered microclimate	Dry condition	Wet condition	Temporary water body
Woodpecker breeding cavities		x	(x)		(x)	x	(x)	(x)					x	x		
Rot holes (containing mould)		x	x	(x)	(x)	x							x	(x)	(x)	
Insect galleries		x				(x)							x	x		
Concavities		x	(x)		(x)	(x)								(x)	(x)	(x)
Exposed sapwood only	x		(x)				(x)	(x)			(x)			(x)	(x)	
Exposed sapwood and heartwood	x	x					(x)	(x)			(x)		(x)	x	(x)	
Crown deadwood	(x)	(x)					(x)	(x)						(x)		
Twig tangles												x				
Burrs and cankers	(x)											x				
Perennial fungal fruiting bodies										x			x			
Ephemeral fungal fruiting bodies and slime molds										(x)						
Epiphytic or parasitic crypto- and phanerogams									x				(x)		(x)	
Nests						x			x				(x)	(x)	(x)	
Microsoil				x	x	(x)									x	
Fresh exudates							(x)	(x)							x	

Table 2
Link between tree-related microhabitats (TreMs) groups and biodiversity in European temperate and Mediterranean forests. ‘x’ indicates that several species of the taxonomic group occur; these species are not necessarily strictly associated with the TreM group. « * » (used for Hymenoptera only) indicates that TreM-associated species are mostly parasitoids. See Appendix A for supporting references and the list of the experts consulted.

	Invertebrates									Vertebrates					Bryophytes	Fungi	Lichens
	Insects						Arachnids		Gastropods	Birds	Mammals			Amphibians & Reptiles			
TreM groups	Coleoptera	Diptera	Hemiptera	Hymenoptera	Lepidoptera	Collembola	Mites	Aranea, & Pseudoscorpionida			Rodents	Bats	Carnivores				
Woodpecker breeding cavities	x	x		x*	x		x	x		x	x	x	x			x	
Rot-holes (containing mould)	x	x		x*		x	x	x	x	x	x	x	x	x	x	x	x
Insect galleries and bore holes	x	x		x*			x	x				x				x	
Concavities	x	x		x*				x		x	x		x	x	x	x	
Exposed sapwood only	x			x	x				x	x		x				x	
Exposed sapwood and heartwood	x	x						x	x	x		x				x	x
Crown deadwood	x	x		x			x	x		x						x	x
Twig tangles								x		x							
Burrs and cankers					x										x	x	
Perennial fungal fruiting bodies	x	x	x	x*	x	x	x		x						x	x	
Ephemeral fungal fruiting bodies and slime molds	x	x	x		x	x	x									x	
Epiphytic or parasitic crypto- and phanerogams	x	x		x	x		x	x	x	x	x		x			x	
Nests	x	x			x		x	x		x	x		x			x	
Microsoil		x				x	x								x	x	
Fresh exudates	x	x		x												x	

Table 3
Hierarchical typology of Tree-related Microhabitats in European temperate and Mediterranean forests. See Table 4 for type definitions and thresholds, and Table 5 for illustrations.

Form	Group	TreM type
Cavities l.s.	Woodpecker breeding cavities	Small woodpecker breeding cavity.
		Medium-sized woodpecker breeding cavity
		Large woodpecker breeding cavity
		Woodpecker "flute" (breeding 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
	Insect galleries and bore holes	Insect galleries and bore holes
	Concavities	Dendrotelm (phytotelmata, water-filled hole)
		Woodpecker foraging excavation
		Trunk bark-lined concavity
		Root buttress concavity
Tree injuries and exposed wood	Exposed sapwood only	Bark loss
		Fire scar
		Bark shelter
		Bark pocket
	Exposed sapwood and heartwood	Stem breakage
		Limb breakage (heartwood exposed)
		Crack
		Lightning scar
		Fork split at the intersection
Crown deadwood	Crown deadwood	Dead branches
		Dead top
		Remaining broken limb
Excrescences	Twig tangles	Witch broom
		Epicormic shoots
	Burrs and cankers	Burr
		Canker
Fruiting bodies of saproxylic fungi and slime moulds	Perennial fungal fruiting bodies (life span > 1y)	Perennial polypore
	Ephemeral fungal fruiting bodies and slime moulds	Annual polypore
		Pulpy agaric
		Pyrenomycete
		Myxomycete
Epiphytic, epixylic and parasitic structures	Epiphytic or parasitic crypto- and phanerogams	Bryophytes
		Foliose and fruticose lichens
		Ivy and lianas
		Ferns
		Mistletoe
	Nests	Vertebrate nest
		Invertebrate nest
	Microsoils	Bark microsoil
		Crown microsoil
Fresh exudates	Fresh exudates	Sap run
		Heavy resinosis
7 forms	**15 groups**	**47 types**

These include the following insect orders: Coleoptera, Diptera, Hemiptera, Hymenoptera, Lepidoptera; and, to a lesser extent, other arthropods such as Collembola and Acari. Vertebrates are also prominent users of TreMs. TreMs also provide very important substrates and colonization entries for wood decaying fungi. However, the number of TreM specialized bryophytes and lichens is limited (Jahns, 1989).

The relationship at the TreM scale between cavity types such as woodpecker breeding cavities, mould cavities or dendrotelms, and the species communities they host is relatively well known and documented (e.g. Gossner et al., 2016; Gouix and Brustel, 2012; Martin and Eadie, 1999; Ranius, 2002). However, knowledge of the communities hosted by other TreM types such as bark microsoil is relatively scarce (Halama et al., 2014).

3. TreM hierarchical typology and protocol guidelines

3.1. Hierarchical typology

Following Larrieu (2016), we adopted a hierarchical approach to build our typology. We first identified seven general forms that share the same physiognomy and functional characteristics. Then, these forms were subdivided into fifteen more specific groups which can be further assigned to 47 distinct types based on morphological characteristics and biodiversity relevance (Table 3):

1. **Cavities** *lato sensu* are basically holes or shelters formed in the wood either by cavity builders (e.g. woodpeckers, saproxylic insects), decay processes (rot hole), morphological particularities on the trunk or collar (e.g. dendrotelms in forks or root-buttress shelters). They provide buffered climatic conditions and nesting sites for a wide array of species, from arthropods to large mammals. They can be subdivided into cavities *stricto sensu* in which the entrance is smaller than its interior diameter, and galleries and concavities if the entrance is of the same or greater width than the interior. This general form is sub-divided into four groups and 15 TreM types.
2. **Injuries** expose sapwood and sometimes also heartwood and create access for colonizing taxa. They are mainly created by mechanical impacts such as trunk or crown breakage from wind, ice or snow, but may also be caused by lightning strikes and frost, and occasionally by forest fires. They encompass two TreM groups and nine types. Exposed wood and injuries may evolve to rot holes over time if the tree is not able to seal the wound.
3. **Crown deadwood** consists of dead branches in general occurring at the top of the tree; this often provides open xero-thermophilous conditions due to the location in the canopy. Crown deadwood may also take the form of large broken branches where a thick dead branch section still remains. Dead tree tops, generally sun-lit, expose the heartwood and offer a transition between the living tree and dead wood. This form contains one TreM group and three types.
4. **Excrescences** are mainly caused by reactive growth to an increase in light availability or to a parasitic or microbial intrusion where the tree creates specific structures to isolate the pathogen (e.g. canker, burr). Excrescences are comprised of two TreM groups and four types.
5. **Fungal fruiting bodies and slime moulds** are the visible part of saproxylic fungi (or fungi-like organisms such as Myxomycetes) and are classified as perennial or ephemeral (lasting less than a year) structures. There are two TreM groups and five types in this general form.
6. **Epiphytic and epixylic structures** encompass a wide variety of structures in which the tree is merely the physical support on which the TreM grows or is located. These structures include different organisms growing on trees (cryptogams and phanerogams), vertebrate or invertebrate nests and also "perched" microsoils (developed from organic material such as leaves, bark, decaying bryophytes, etc.) either on trunk bark, at fork intersections or on a flat area within the crown. This general form is sub-divided into three TreM groups and nine types.
7. **Exudates** are sap runs or heavy resinosis and encompass one TreM group and two types

For each TreM type, we provide a definition (Table 4) and an

Table 4
Tree related Microhabitat type definitions and inventory thresholds (Ø: diameter) for European temperate and Mediterranean forests.

Type	Definition	Size threshold for inclusion in surveys	Threshold choice
Small woodpecker breeding cavity	Cavity entrance ø < 4 cm. The breeding cavity of *Dendrocopos minor* is usually drilled in a dead branch.	Cavity entrance ø < 4 cm	Biological, woodpecker size
Medium-sized woodpecker breeding cavity	Round cavity entrance about ø = 4–7 cm. The breeding cavities of the medium-sized woodpeckers (*Dendrocopos major*, *D. medius*, *D. leucotos*, *D. syriacus*, *Picus viridis*, *P. canus*, *Picoides tridactylus)* are usually drilled into decaying wood (dead branch, snag, insertion of broken-off branches).	Cavity entrance ø = 4–7 cm	Biological, woodpecker size
Large woodpecker breeding cavity	Oval cavity entrance ø < 10 cm. The breeding cavities of *Dryocopus martius* are usually drilled on the main part of the trunk (without branches).	Cavity entrance ø > 10 cm	Biological, woodpecker size
Woodpecker “flute” (string of ≥3 breeding cavities))	At least three woodpecker breeding cavities in line on the trunk. Maximum distance of 2 m between two consecutive cavities.	Cavity entrance ø > 3 cm	Biological, woodpecker size
Trunk base rot-hole	Cavity chamber is completely protected from surrounding microclimate and rain Top-closed trunk cavity containing more or less mould (depending on its development stage). The cavity bottom has ground contact. Note that the cavity entrance can be higher on the trunk.	Opening ø > 10 cm	Biological, mammal size
Trunk rot-hole	Top-closed trunk cavity containing more or less mould (depending on its development stage). The cavity bottom has no ground contact.	Opening ø > 10 cm	Biological, mammal size
Semi-open trunk rot-hole	Cavity chamber is not completely protected from surrounding microclimate and rain may flow in. Note that the cavity entrance can be higher up in the trunk	Opening ø > 30 cm	Pragmatic
Chimney trunk base rot-hole	Cavity in the trunk of the tree that is completely open at the top, often resulting from stem breakage; the cavity base reaches ground level, so the inner cavity is in direct contact with the soil.	Opening ø > 30 cm	Pragmatic
Chimney trunk rot-hole	Cavity in the trunk of the tree that is completely open at the top, often resulting from stem breakage; the cavity base does not reach ground level, so the inner cavity is not in direct contact with the soil.	Opening ø > 30 cm	Pragmatic
Hollow branch	Rot hole in a large brach, resulting in a tubular shelter, often horizontally oriented.	Opening ø > 10 cm	Pragmatic
Insect galleries and bore holes	A bore hole network of xylophagous insects indicates a wood hole system. An insect gallery is a complex system of holes and chambers created by one or more insect species in the wood.	Hole ø > 2 cm or numerous smaller holes covering an area > 300 cm^2 (A5 format)	Pragmatic
Dendrotelm (phytotelmata, water-filled hole)	Cup-shaped concavity that, due to its form, retains water until it dries out by evaporation.	ø > 15 cm	Biological, assemblage type
Woodpecker foraging excavation	Concavity resulting from the foraging activities of woodpeckers. The excavation is conical: the entrance is larger than the interior.	Depth > 10 cm, ø > 10 cm	Biological, bird size
Trunk bark-lined concavity	Natural bark-lined concavity on the tree trunk. No mould.	Depth > 10 cm, ø > 10 cm	Biological, bird size
Root buttress concavity	Natural bark-lined concavity at the base of the tree trunk formed by the tree roots and the soil. No mould (if so: see Trunk base rot hole)	Entrance ø > 10 cm	Pragmatic
Bark loss	Loss of bark exposing sapwood (skinning caused e.g. by felling, skidding, natural tree fall, rock fall, rodents).	Area > 300 cm^2 (A5 format)	Pragmatic
Fire scar	Fire scars on the lower trunk. They usually have a triangular shape and are located at the base of the tree on the leeward side. Fire scars are associated with charcoal and sometimes resin flow on exposed sapwood or bark.	Area > 600 cm^2 (A4 format)	Pragmatic
Bark shelter	Space between peeled-off bark and sapwood forming a shelter (open at the bottom).	Gap > 1 cm; depth > 10 cm; height > 10 cm	Biological, Bat size
Bark pocket	Space between peeled-off bark and sapwood forming a pocket (open at the top) possibly containing mould.	Gap > 1 cm; width > 10 cm; height > 10 cm	Pragmatic
Stem breakage	The stem has broken off but the tree is still alive. The lower part of the deadwood is in contact with living wood with sap flow.	Stem ø > 20 cm at the broken point	Pragmatic
Limb breakage (heartwood exposed)	Exposed heartwood through limb or fork breakage. The wound is surrounded by living wood with sap flow.	Area of exposed heartwood > 300 cm^2 (A5 format)	Pragmatic
Crack	Crack through the bark and the wood (if caused by lightning strike, see below).	Length > 30 cm; width > 1 cm; depth > 10 cm	Biological, Bat size
Lightning scar	Crack caused by lightning strike; usually spiraling around the tree with splintered wood present.	Length > 30 cm; width > 1 cm; depth > 10 cm	Biological, Bat size
Fork split at the insertion	Crack at the insertion of a fork. (If one side of the fork has broken off, see Stem breakage).	Length > 30 cm	Pragmatic
Dead branches	Dead branches located in the canopy, conditions remain relatively shady.	Branch ø > 10 cm, or Branch ø > 3 cm and > 10% of the crown is dead	Pragmatic
Dead top	The entire top of the tree is dead; the deadwood is sun-exposed	ø > 10 cm at the lower part of the piece of deadwood	Pragmatic
Remaining broken limb	A limb has broken off. The remaining end may be splintered. The injury does not affect the trunk (If so, see Stem breakage).	Limb ø > 20 cm at the broken end; length of the remaining piece > 0,5 m	Pragmatic
Witch broom	Dense agglomeration of twigs on branches.	Largest ø > 50 cm	Pragmatic
Epicormic shoots	Dense agglomeration of twigs along the trunk.	> 5 twig clusters	Pragmatic
Burr	Proliferation of cell growth with rough bark	Largest ø > 20 cm	Pragmatic
Decayed canker	Decayed canker. Sapwood exposed. Caused by e.g. *Melampsorella caryophyllacerum*, *Nectria* l. s.	Largest ø > 20 cm or large part of the trunk covered	Pragmatic

(continued on next page)

Table 4 *(continued)*

Type	Definition	Size threshold for inclusion in surveys	Threshold choice
Perennial polypore	Tough fruiting bodies of perennial polypores, showing distinct annual tube layers. Main perennial genera: *Fomitopsis* pp, *Fomes*, *Perreniporia* pp., *Oxyporus*, *Ganoderma* pp, *Phellinus*, *Daedalea*, *Haploporus*, *Heterobasidion*, *Hexagonia*, *Laricifomes*, *Daedleopsis*.	Largest ø > 5 cm	Pragmatic
Annual polypore	Fruiting bodies of annual polypores, lasting several weeks. The European annual polypores have only one layer of tubes and are usually elastic and soft (no woody parts). Main annual genera: *Abortiporus, Amylocystis, Bjerkandera, Bondarzewia, Cerrena, Climacocystis, Fistulina, Gloeophyllum, Grifola, Hapalopilus, Inonotus, Ischnoderma, Laetiporus, Leptoporus, Meripilus, Oligoporus, Oxyporus, Perenniporia pp, Phaeolus, Piptoporus, Podofomes, Polyporus, Pycnoporus, Spongipellis, Stereum, Trametes, Trichaptum, Tyromyces*.	Largest ø > 5 cm or cluster of > 10 fruiting bodies	Pragmatic
Pulpy agaric	Large, thick and pulpy or rather fleshy fruiting body of gill-bearing fungi (order Agaricales). E.g.: *Armillaria, Pleurotus, Pholiota*, or large *Pluteus* species. The fruiting body generally remains several weeks.	Largest ø > 5 cm or cluster of > 10 fruiting bodies	Pragmatic
Pyrenomycete	Tough hemispheric dark fungi ressembling a lump of coal. E.g: *Daldinia* or *Hypoxylon*.	Stroma ø > 3 cm or stroma cluster covering > 100 cm^2	Pragmatic
Myxomycete	Amoeboid slime mold which forms moving plasmodium. The plasmodium is gelatinous when fresh.	Largest ø > 5 cm	Pragmatic
Bryophytes	Trunk covered by mosses and liverworts.	> 10% of the trunk area covered	Pragmatic
Foliose and fruticose lichens	Trunk covered by foliose or fruticose lichens.	> 10% of the trunk area covered	Pragmatic
Ivy and lianas	Lianas and other climbing phanerogams (*Hedera helix, Clematis vitalba, Lonicera periclimenum, Vitis vinifera*).	> 10% of the trunk area covered	Pragmatic
Ferns	Ferns growing directly on a part of a tree (i.e. epiphyte)	> 5 fronds	Pragmatic
Mistletoe	Hemiparasitic plants (*Viscum* spp., *Arceuthobium oxycedri, Loranthus europaeus*).	Largest ø > 20 cm for *Viscum* spp. and *Loranthus europaeus*; more than 10 clusters for *Arceuthobium oxycedri,*	Pragmatic
Vertebrate nest	Nest built by birds, dormice, mice or squirrels.	ø > 10 cm	Biological, animal size
Invertebrate nest	Larval nest of invertebrates: e.g. Pine processionary moth *Thaumetopoea pityocampa*, wood ant *Lasius fuliginosus* or wild bees *Apis mellifera*.	Presence (observation of nest or associated insects)	Pragmatic
Bark microsoil	Microsoil resulting from micro-pedogenesis of epiphytic mosses, lichens or algae and necrosed old, thick bark.	Presence (direct observation or specific fungi)	Pragmatic
Crown microsoil	Microsoil resulting from pedogenesis of debris and litter fallen from the crowns, often colonized by roots of the TreM bearing-tree. Main positions: flat areas on limbs, forks, sometimes stem junctions of twin trees.	Presence	Pragmatic
Sap run	Fresh significant flow of sap.	Length > 10 cm	Pragmatic
Heavy resinosis	Fresh significant flow of resin.	Length > 10 cm	Pragmatic

illustration (Table 5) to facilitate correct field identification. For each type, we define a minimum threshold size for recording and monitoring purposes. These thresholds are based on biological features whenever possible (e.g. the size of the woodpecker species that builds a given type of cavity, Table 2), or a pragmatic approach was taken to allow for standardized inventories and reduce observer effect and observation time.

The classification into general forms (n = 7), TreM groups (n = 15) and TreM types (n = 47) provides three hierarchical aggregation levels (grains) to be used differently depending on the aim of a given study, inventory or monitoring process. For example, the general form level can easily be applied for quickscans and for selecting habitat trees during tree marking and felling in managed forests; however, this grain is not fine enough for detailed monitoring. Thanks to the hierarchical structure, inventories with a finer grain can always be aggregated to a coarser level to merge different sources of information or compare different forests. Furthermore, the hierarchy presented should not prevent any user from adopting an even finer grain with more levels (see below).

3.2. Protocol guidelines for standardized TreM surveys

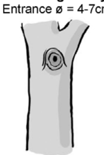
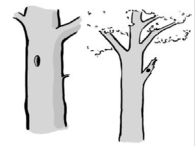
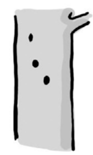
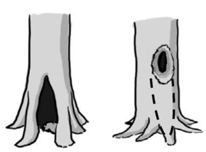
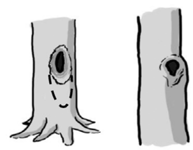
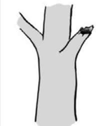
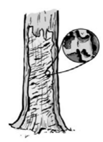
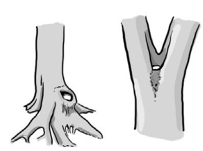
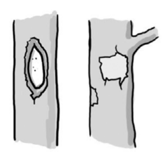
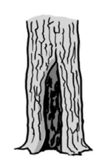
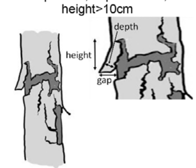
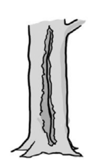
In order to produce standardized and comparable TreM surveys, a certain number of standardized inventory protocols must be applied to the unequivocal definitions and threshold sizes of the TreM types detailed above.

A wide range of survey approaches can be applied, depending on specific objectives, requirements or circumstances. However, some basic rules should be respected in order to perform quality TreM surveys with limited observer effects (Paillet et al., 2015a) and high reliability (accuracy, repeatability and practical performance). We have assumed that classical forest protocols already include basic tree data such as diameter at breast height (dbh), tree species and status (dead or alive). TreM records will therefore complement this classical survey data. Based on this assumption, we propose a set of requirements (i.e. field methods, equipment and recommended thresholds) that are to be met, in order to allow *a posteriori* compilation and comparison of datasets including TreM inventories. For the most detailed and intensive survey level (e.g. scientific studies), we also specify additional features that could complement TreM inventories for a finer description and characterisation of specific TreM types (Appendix B).

3.2.1. TreM inventories: survey baseline

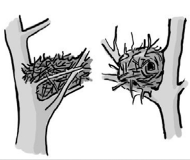
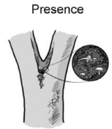
The three levels of the hierarchical typology reflect three specific survey objectives: (i) the first level (i.e. Forms) could be used for quickscans of TreM-bearing trees during forest management operations (e.g. tree selection and marking); (ii) the second level of hierarchy (i.e. Groups) could be applied in routine surveys and inventories (NFI, management plan and Natura 2000 inventories); (iii) the third, most detailed, level (i.e. Types) could be applied in scientific surveys, with the possibility, depending on the objective of the study, to further subdivide and characterise the individual TreMs (according to the

Table 5
Illustrations of the TreM types in European temperate and Mediterranean forest.

Form	Group	Types					
Cavities l.s.	Woodpecker breeding cavities	**Small woodpecker breeding cavity** Entrance ø<4cm 	**Medium-sized woodpecker breeding cavity** Entrance ø = 4-7cm 	**Large woodpecker breeeding cavity** Entrance ø >10cm 	**Woodpecker flute** Entrance ø > 3cm 		
	Rot-holes	**Trunk base rot-hole (closed top, ground contact)** Opening ø >10cm 	**Trunk rot-hole (closed top, no ground contact)** Opening ø >10cm 	**Semi-open trunk rot-hole** Opening ø >30cm 	**Chimney trunk base rot-hole** Opening ø >30cm 	**Chimney trunk rot-hole** Opening ø >30cm 	**Hollow branch** Opening ø >10cm 
	Insect galleries	**Insect galleries and bore holes** Hole ø >2cm or area >300cm² 					
	Concavities	**Dendrotelm** ø >15cm 	**Woodpecker foraging excavation** Depth >10cm, ø >10cm 	**Trunk bark-lined concavity** Depth >10cm, ø >10cm 	**Root-buttress concavity** Entrance ø >10cm 		
Tree injuries and exposed wood	Exposed sapwood only	**Bark loss** Area > 300cm² 	**Fire scar** Area > 600cm² 	**Bark shelter** Gap >1cm, depth >10cm, height>10cm  	**Bark pocket** Gap >1cm, width >10cm, height>10cm  		
	Exposed sapwood and heartwood	**Stem breakage** ø >10cm at break point 	**Limb breakage** Exposed heartwood >300cm² 	**Crack** Length > 30 cm, width > 1 cm, depth > 10 cm 	**Lightning scar** Length > 30 cm, width > 1 cm, depth > 10 cm 	**Fork split at insertion** Length > 30 cm 	
Crown deadwood	Crown deadwood	**Dead branches** Branch ø >10cm, or Branches ø >3cm and >10% of the crown is dead 	**Dead top** ø >10cm at the base of the piece of deadwood 	**Remaining broken limb** broken end ø >20cm, length of the remaining piece >0.5m 			

(continued on next page)

Table 5 *(continued)*

Form	Group	Types					
Excrescences	Twig tangles	**Witch broom** Largest ø >50cm 	**Epicormic shoots** >5 twig clusters 				
	Burrs and cankers	**Burr** Largest ø >20cm 	**Canker** Largest ø >20cm or large part of the trunk covered 				
Fruiting bodies of saproxylic fungi and slime moulds	Perennial fungal fruiting bodies	**Perennial polypore** Largest ø >5cm 					
	Ephemeral fungal fruiting bodies	**Annual polypore** Largest ø >5cm or cluster of > 10 fruiting bodies 	**Pulpy agaric** Largest ø >5cm or cluster of > 10 fruiting bodies 	**Large Pyrenomycete** Stroma ø >3cm or stroma cluster covering >100cm² 	**Myxomycetes** Largest ø >5cm 		
Epiphytic and epixylic structures	Epiphytic and parasitic crypto- and phanerogams	**Bryophytes** >10% of the trunk area covered 	**Foliose and fruticose lichens** >10% of the trunk area covered 	**Ivy and lianas** >10% of the trunk area covered 	**Ferns** > 5 fronds 	**Mistletoe** Largest ø >20cm 	
	Nests	**Vertebrate nest** ø >10cm 	**Invertebrate nest** Presence 				
	Microsoils	**Bark microsoil** Presence 	**Crown microsoil** Presence 				
Exudates	Exudates	**Sap run** Cumulative length >10 cm 	**Heavy resinosis** Cumulative length >10 cm 				

elements indicated in Appendix B, see below).

Ideally, TreM inventories should be made by a team of two observers, especially for routine inventories and scientific surveys. Even though a single trained observer may be able to perform a good survey, double observation is assumed to be more complete and systematic and to reduce observer effects (Paillet et al., 2015a). Every eligible tree is visually checked for TreMs from all directions from the root base up to the crown. One thorough inspection from all sides may be sufficient, but we suggest a minimum of two turns around a tree (e.g. one for the trunk base and lower trunk up to eye-level, and another one to inspect the upper trunk and tree crown); this may sometimes be difficult and time-consuming when the field conditions are rough (e.g. steep slope). Individual tree surveys may take from one to three minutes, depending on the slope, tree dimensions and level of detail required (i.e. the typology grain selected). This time per tree is only an estimation based on field experience and should be confirmed by field trials applied to a specific objective (e.g. surveys by NFI teams).

During routine inventories, no specific field equipment is required other than binoculars, which are essential for checking TreMs high on the trunk or in the tree crown, especially smaller features such as branch cavities or breeding cavities of medium-sized woodpeckers. For more intensive surveys like detailed cavity studies, other tools such as pole cameras or drones (Steich et al., 2016) may be helpful in assessing the characteristics of cavities (inner volume, presence/absence of mould). In broadleaved-dominated stands, it is highly advisable to record TreMs only after leaf fall because some small TreMs high in the canopy (dead branches, epiphytes) are difficult to see through the tree's leaves; a high, thick understory often limits visibility as well.

The present recommendations do not impose any dbh or height threshold for TreM inventories. The 'relevant' dbh threshold will depend on the specific objectives and local circumstances, but it should be borne in mind that the higher the threshold, the fewer the trees checked, and the lower the workload. For comparative studies, the dataset with the highest dbh or height threshold value will logically determine the subset of data that can be used for comparison. Furthermore, even if the proportion of TreM-bearing trees increases dramatically with increasing dbh class (Larrieu and Cabanettes, 2012; Michel et al., 2011; Paillet et al., 2017; Winter et al., 2015b), medium-sized trees may account for a significant proportion of certain types (Larrieu et al., 2012; Paillet et al., 2017). Therefore, minimum dbh-limit should not be above 30 cm; we recommend lower values (e.g. 10 cm dbh), particularly for research surveys.

Observed TreMs may be listed per tree (occurrence) or counted (abundance on each tree) in a quantitative (e.g. number of conks or woodpecker cavities, etc.) or semi-quantitative way (e.g. percentage classes of exposed heartwood). Most TreMs can be recorded for both living trees and snags (Table 4). However, some TreM types occur on living trees only (e.g. sap runs, mistletoe).

3.2.2. Optional TreM features for intensive surveys

Observing TreM attributes in detail will provide a better understanding of TreM dynamics, both at the TreM scale (i.e. evolving or decay processes) and at the stand scale (i.e. TreM profile dynamics). We present in Appendix B an extensive set of recordable attributes for each TreM. The set covers additional size specifications (inner and outer dimensions), decay stage, position on the tree, content (e.g. amount of mould in rot holes) and other TreM characteristics (e.g. simple vs splintered for trunk breakage). These attributes may be recorded during intensive monitoring or research operations since they may be of particular importance for specific taxa. They may also be considered as TreM sub-types, though we did not include them as such in this typology in the interest of simplicity. For each quantifiable feature, we propose recording either the absolute dimension (size, height, surface area) or using a semi-quantitative scale (e.g. cover classes, 10-25% of the total trunk area…). For some TreM types, we also suggest setting additional thresholds or further spliting down size classes to record smaller-sized features. Three drawing referentiels are also proposed to quickly identify evolving stages of rot holes and bark loss, and life stages of perennial polypores (Appendix B).

4. Discussion

4.1. To include or not to include: TreM definition and typology relevance

Establishing standards and typologies is a prerequisite for any type of monitoring. The typology we present in this paper with its 47 TreM types should help standardize TreM inventories and make comparative studies possible. To build this typology, we used mainly morphological characteristics to categorize the TreMs since morphology is the simplest criterion to differentiate such structures in the field. Second, we categorized TreM groups by the substrates they supply. To determine the eligibility of a given TreM to the typology and its hierarchical position, we primarily considered its taxa relevance and its pertinence in terms of their life-history traits (e.g. the Frisbee database, Bouget et al., 2008, for saproxylic beetles; or Syrph the Net, Speight et al., 2013, for hoverflies). We carried out exploratory clustering analyses based on the substrates supplied (Larrieu, 2014) and on complementary expert knowledge.

Such a typology may appear too simplistic as a surrogate for direct biodiversity assessment since several species groups such as arthropods select their habitats according to their chemical markers (for example, emanations from the decaying process; see e.g. Gouix, 2011), rather than their physical features (e.g. Schmidl et al., 2008). To cope with this limitation, supplementary attributes (e.g. epiphyte hiding the entrance of a woodpecker breeding cavity) or characteristics (e.g. sun-exposed vs shaded dead branches) could be inventoried in intensive studies to differentiate species assemblages that coexist within the same TreM type. This may help to specify the functional links between biodiversity and TreM substrates. However, many TreM types could also be viewed as a composite of several subtypes that are impossible to delineate individually in the field, despite their importance for certain highly specialized taxa (such as the different beetle assemblages living in the three parts of a conk of saproxylic fungi: the trama, the pores or the interface between the conk and the bark, see e.g. Nikitsky and Schigel, 2004).

Inversely, the typology may appear too detailed for some practitioners. Here, its hierarchical structure provides adaptability to various contexts and objectives. In particular, information from different studies or inventories can always be aggregated to a coarser grain in the topology in a coherent and compatible way in order to compile and compare different datasets (see e.g. Larrieu et al., 2014b).

4.2. Relevance of thresholds and guidelines

In theory, to fully assess the role TreMs play in biodiversity, all the TreMs on a given tree should be recorded, whatever their size or position, since they all provide resources for associated communities. This means, however, that there would be an infinite number of TreMs for a given tree. In practice, comprehensive recording of TreMs is virtually impossible and, even with simplified lists, observer effects are strong (Paillet et al., 2015a). It is therefore crucial to define thresholds in order to reduce (i) the time devoted to the survey, and (ii) the observer-related biases. Definiting thresholds increases replicability and thereby improves the quality of the data. Most of the thresholds we have defined here are based on recording practicality ("pragmatic" thresholds, e.g. a minimum area of a missing bark for observing it easily whatever its position on the trunk), though thresholds for 13 TreM types are based on biological evidence and features (such as the mean diameter of a breeding cavity for a woodpecker species). A few focus on a target taxon (e.g. thresholds for crack width correspond to bat species requirements). We feel that both threshold parameters and a description of features are essential to standardize the records. Including these two types of data makes a clear and unequivocal delineation for TreM records possible and allows comparisons to be made among different studies throughout European forests. These proposed thresholds may be modified in the future if other values are found to be more ecologically relevant (i.e. based on scientific evidence) but, in case of changes, sensitivity analyses should be performed to be sure that detectability levels in the field remain acceptable. In other words, the typology presented in this paper may be adapted as scientific knowledge develops, but with respect to the proposed hierarchical approach.

It may not always be possible to restrict TreMs surveys to periods after leaf fall, for example, in particular contexts (e.g. in mountain forests where inventories are preferably performed in summer), stand types (e.g. those dominated by evergreen broadleafs or conifers) or wide-scale inventories (a significant proportion of National Forest Inventories are performed during the vegetation period). TreM records during the vegetation period require more time to reliably check the tree and may make recording certain TreM types very difficult (e.g. crown cavities). Inversely, some types, such as crown deadwood on living trees, may be easier to identify during the vegetation period. In any case, as inventories are performed at different periods of the year, the date of inventory should be included in subsequent analyses to correct for possible variations due to potential observation biases.

The part of the tree that is to be observed during TreM surveys can also be adapted. Branches (and leaves on conifers and evergreen species) can hide parts of the trunk; therefore recording TreMs on the trunk only would be time–saving and would minimize potential observer effect. Moreover, close range observation does not require binoculars and reduces the risk of misinterpretation (e.g. dendrotelms). However, few TreM types are exclusively found on the lower part of the trunk (e.g. root-buttress concavities) and certain TreM types are specific to the crown (e.g. witch brooms). Furthermore, cavities suitable for bats are mainly borne by large healthy branches (e.g. Tillon and Aulagnier, 2014), and crown deadwood hosts very specific beetle assemblages (Bouget et al., 2011). We recommend observing at least the whole trunk from the ground to the crown base and its main sub-vertical limbs, and to complete the inventory by recording crown deadwood.

4.3. Limitations of the typology

The typology presented herein is mainly valid for European temperate and Mediterranean forests; indeed, the scientists co-authoring this paper are experts in this field. As a consequence, TreMs specific to other forest types might be under-represented. For example, in this typology, only one TreM type (fire scars) has a charred wood substrate, while TreMs linked to wildfire certainly provide valuable substrates for a large number of species in the boreal biome, where wildfires are typical (e.g. Gibb et al., 2006; Hjältén et al., 2012). This is probably also true for the Mediterranean biome, though to a lesser extent (Bouget et al., 2008). Similarly, since woodpeckers do not occur in Australasia (Cockle et al., 2011), the TreM group *woodpecker breeding cavities* is not relevant for e.g., Australian temperate forests. However, our typology is flexible enough to be complemented and further adapted for use in forest types outside our initial predefined area of application, at least in boreal or non-European temperate forests.

We also designed this typology mainly for living trees and standing deadwood. However, certain TreMs may also occur on lying deadwood. For example, conks of fungi, Myxomycetes, dendrotelms or woodpecker feeding holes regularly occur on lying pieces of deadwood (Bobiec et al., 2005), and contribute to the total supply at the stand scale. Furthermore, lying deadwood contains microhabitats that are not covered in this typology (e.g. specific mould and microsoil conditions of highly decayed wood, pit and mound structures and microtopographies). Therefore, recording TreMs on standing trees only (living and dead) may lead to an underestimation of what should be taken into account in studies which focus on the relationship between TreMs and biodiversity at the stand scale. In this case, sampling should include TreMs on lying deadwood and the typology should be adapted accordingly.

4.4. Perspectives for research

4.4.1. TreMs and environmental characteristics

At the tree scale, the link between TreM richness or diversity and tree characteristics, e.g. trunk diameter or tree vitality, has already been studied (Larrieu and Cabanettes, 2012; Larrieu et al., 2014a; Vuidot et al., 2011; Winter et al., 2015b; Winter and Möller, 2008). However, these studies concern only a limited number of tree species (mainly *Fagus sylvatica* L. and *Abies alba* Mill.). In addition, the links between TreMs and tree characteristics are likely to vary with site and climatic conditions such as soil type and fertility, elevation and humidity; other abiotic factors such as rockfalls, avalanches and snow or thunderstorms can also generate TreMs. The effects of these environmental factors on TreM development have rarely been studied due to the limited number of large datasets (either in number of observations or spatial extent) and to the difficulty of clearly identifying the origin of certain TreMs. A few studies have tested co-occurrences and correlations among TreMs (e.g. Larrieu and Cabanettes, 2012; Regnery et al., 2013b; Winter et al., 2015b) but, in order to better understand how TreMs appear and change over time, these studies should be complemented by further comparable tests, based, whenever possible, on data from long-term surveys on permanent plots. Ultimately, this would make it possible to simplify the typology based on co-occurrence patterns.

At the stand scale, Bouget et al. (2014), Larrieu et al. (2012), Larrieu et al. (2016), Michel and Winter (2009), Paillet et al. (2017), and Winter et al. (2005) have investigated how TreM profiles are affected by setting aside forest reserves and by time since management abandonment. Indeed, there is a general trend towards higher densities of TreMs in strict reserves and when forests have been left unmanaged for a long time. But studying only TreM densities rather than the TreM profile may mask compensations between TreM types typical for managed or unmanaged sites; and the response may vary with the indices used (i.e. abundance vs. occurrence data). For example, Paillet et al. (2017) showed that the overall density of TreMs at the stand level was higher in strict forest reserves than in their managed counterparts and that the magnitude of this difference varied with elevation. Conversely, Larrieu et al. (2012) showed that the number of TreMs was not always higher in unmanaged stands since dendrotelms and missing bark were favoured by logging; however, they did find that TreM diversity was lower in managed stands than in near-natural forests. To confirm these findings, reference studies in the rare primeval temperate forests, in Europe or elsewhere, are much needed (see e.g. Commarmot et al., 2013). Studying remnants of primeval forests could also help us understand the spatial distribution of TreMs under natural conditions. More generally, the effects of different management types (silvicultural regimes) on TreMs have rarely been tested (Michel and Winter, 2009). Finally, microhabitat dynamics have not been studied over time. Long-term monitoring or modeling is necessary to better understand the genesis and mechanisms that drive microhabitat dynamics (see Siitonen, 2012).

4.4.2. TreMs and biodiversity

Some TreM types (e.g. mould cavities) harbour high species richness and host many different taxonomic groups, while some TreM types (e.g. dendrotelms) harbour few species belonging to only a few taxonomic groups. Nevertheless, conservation value cannot only be defined by the number of species using a given TreM type; we should also consider the occurrence of species exclusively conditioned to a single TreM type. That is why we combined scientific information and expert knowledge to build a typology based on TreM substrate availability and biodiversity relevance.

At the stand scale, most of the references related to the ecological role of TreMs are limited to certain forest ecosystems and taxonomic groups, mainly saproxylic beetles (e.g. Bouget et al., 2014; Bouget et al., 2013; Lassauce et al., 2013; Winter and Möller, 2008) and hoverflies (e.g. Herrault et al., 2016; Larrieu et al., 2015) in temperate forests, and birds and bats (e.g. Regnery et al., 2013a) in Mediteranean forests. Evidently, the link between some species groups and TreM types remains unknown or requires stronger scientific evidence. Specific research (i.e. correlative analyses at tree and stand scales) is still needed to confirm the role of certain TreMs as a substrate for biodiversity in European forest ecosystems. In particular, analyzing TreM characteristics as specified in Appendix B may help us better understand the ecological mechanisms involved in the relation between TreM substrates and biodiversity.

At the landscape scale, very few studies have assessed the effects of TreM densities on biodiversity, with the following exceptions: cavities and birds (e.g. Robles and Martin, 2014), hollow trees and beetles (e.g. Ranius et al., 2010), and a set of TreM types and hoverflies (Herrault et al., 2016). In particular, it is unclear wether a single tree bearing a combination of TreM types is equivalent to several trees bearing the same combination of single TreM types. This question, also referred to as the SLOSS – Single Large Or Several Small − debate (Ovaskainen, 2002; Tjørve, 2010), has, to our knowledge, not been assessed in European forests (but see Le Roux et al., 2015 for an example in Australia). More information is therefore needed to determine the density and spatial distribution of TreMs required to conserve their associated biodiversity or to enhance populations of rare or endangered specialized species.

5. Conclusions: Tree related Microhabitats as a monitoring and management tool

For forest managers, TreMs have long been seen as damage or defects to trees which negatively affect timber production. Especially where high quality timber was the main production goal, trees with high TreM potential such as forked, leaning or bizarrely shaped trees (Bütler et al., 2013) and so called "wolf trees" (with undesired overgrowth) were subject to negative selection when competing with trees of promising quality. Additionally, old senescent trees as well as snags are often considered hazardous to workers and the public and are systematically removed. Thus, TreM-bearing habitat trees are currently rare in managed forests in Europe (Bütler and Lachat, 2009; Larrieu et al., 2014a; Larrieu et al., 2012; Larrieu et al., 2014b; Paillet et al., 2017; Winter and Möller, 2008). Furthermore, the situation is likely to deteriorate if positive selection strategies are not applied more widely to secure a continuous supply of trees with TreM potential along with the production of merchantable trees. Nowadays, however, the retention of habitat trees (including TreMs-bearing trees) is increasingly being recognized as necessary, both in forest management (Kraus and Krumm, 2013) and policy (Ministerium für Landwirtschaft Umweltschutz und Raumordnung, 2004; Winter et al., 2015a). TreMs' ecological value is increasingly being emphasized, and efforts are being made to integrate their conservation into modern multi-functional forestry (Bütler et al., 2013; Flade et al., 2004; Larrieu et al., 2014a; Michel and Winter, 2009; Winter et al., 2015a). In particular, the Natura 2000 European network promotes the conservation of habitat trees as a tool to ensure the long term survival of threatened species, but the characterizations of habitat trees and microhabitats remains rather vague and heterogeneous (European Commission, 2015).

Our proposed TreM definition and typology, along with our guidelines for standardized survey protocols, represent a first step towards a standardized method for inventorying TreMs and conserving of habitat trees. This work will ensure reproducibility and high data quality, and aims to provide a basic guarantee that the methods used to gather data by various operators are standardized (Allegrini et al., 2009; Ferretti, 2009, 2013; Paillet et al., 2015a). In particular, we expect that implementing the typology at various scales and for various purposes will make data comparable across national inventories, and help establish references at a large international scale. The list is open and adapted to further developments based on increasing scientific knowledge, as suggested above. However, we believe the typology in its current form is already valid, particularly for scientific studies and monitoring purposes, and can henceforth be used to evaluate the success of policies designed to achieve nature conservation. Indeed, Kraus et al. (2016)'s European TreM field guide initiative is largely based on the present work and has already been translated into several languages and applied in a wide range of ecological conditions (see also the tablet and smartphone applications used to vulgarize TreMs, available at http://www.integrateplus.org/m-learning-tools.html).

The present study clearly shows that TreMs support a wide array of biodiversity that is not usually supported by other forest structures. From a monitoring point of view, information about TreMs is complementary to data on features traditionally classified under forest structure (dimensions, tree species) and deadwood (type, dimension, decay stage). Understanding the factors that influence the occurrence and distribution of TreMs, their link with biodiversity and quantifying the potential observer effect would ultimately help validate TreMs as biodiversity indicators (Paillet et al., 2015a). In particular, comparing the performance of TreMs with that of other indicators (e.g. those used for reporting on the State of Europe's Forests) is much needed (Gao et al., 2015). We expect TreMs to play a complementary (or combined) role with other existing biodiversity indicators such as deadwood profile or tree species diversity. Integrating TreM preservation into common forest management practices may help slow forest biodiversity loss while TreM monitoring may prove to be an additional tool for assessing the state of biodiversity in European forests.

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Appendix A. and B Supplementary data

Supplementary data associated with this article can be found, in the online version, at http://dx.doi.org/10.1016/j.ecolind.2017.08.051.

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