

Know, protect and promote habitat trees

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Fig. 1. An exemplary habitat tree! Only the oldest and thickest trees show a large number and variety of tree-related microhabitats.

Biodiversity is of great importance for the functioning of the forest ecosystem. Habitat trees (Fig. 1) are a key component of forest biodiversity. Experts from Europe have developed a typology of tree-related microhabitats, small life-sites borne by some trees, which are indispensable for thousands of specialised organisms. The uniform use of the forms, groups and types of these tree-related microhabitats facilitates the implementation of recommendations in forestry practice. In addition, these standardised data can be used for monitoring forest biodiversity or for evaluating the success of measures to promote biodiversity in forests.

The vast majority of European forests are managed, and they provide services for humans as diverse as timber production, protection against natural hazards and recreation. Forests also play an important role in preserving biodiversity. However, natural forest development in commercial forests is very limited. The focus of management is usually on the establishment and growing phases, while the ageing, decay and regeneration phases are kept as short as possible or are skipped completely. There is often, therefore, a lack of old trees and dead wood. However, forest biodiversity can be successfully preserved and promoted with appropriate management measures and instruments. Old and large trees, which often have special features

such as cavities, play a key role in this context: these habitat trees are a critical component of forest biodiversity and their presence in commercial forests depends strongly on the actions of the forest managers. The vital role of habitat trees for biodiversity and their importance for the resilience of forests is increasingly being recognised and taken into account in forest management.

Habitat trees – tree-related microhabitats

A habitat tree is a living or dead standing tree that bears at least one microhabitat. The term microhabitat refers to very small-scale or specially delimited habitats. Tree-related microhabitats (often abbreviated as TreMs in the following) are clearly delimited structures supported by the tree, on which many different, sometimes highly specialised animal, plant, lichen and fungal species depend for at least part of their life cycle (LARRIEU *et al.* 2018, Fig. 2). They are produced, for example, by injuries caused by rockfall, lightning or woodpecker activities. TreMs can also be elements for which the tree merely serves as a support, such as nests, ivy or lianas.

In the past, the term “wildlife tree” was also used for habitat trees or for trees with nests of tree-nesting birds and “veteran tree” used for remarkably old or large trees.

TreMs are important refuge, breeding, wintering and feeding spots. Each species prefers to live in a specific TreM. A diversity of TreMs within a forest stand meets the specific requirements of many different species. The more numerous the species are, the more ecological functions they can fulfil, such as pollination, wood decomposition and regulation of species with large population dynamics. If many species perform the same function, this is tantamount to insurance: if one species fails temporarily, another can step in and take over the function (YACHI and LOREAU 1999). It is therefore beneficial for the functioning of the forest ecosystem to have as many species as possible, even inconspicuous ones. For this purpose TreMs are needed.

Age, diameter and tree species influence tree-related microhabitats and the associated biodiversity

Throughout its life every tree is exposed to random events, for example, rockfall,

storms, lightning or fire, the falling of a neighbouring tree, wet snow, colonisation by fungi, or the chiselling of woodpeckers. These events leave behind bark damage, broken branches, cavities and so on. With increasing age and diameter of a tree, the number and diversity of TreMs it harbours therefore increases significantly (BÜTLER and LACHAT 2009; VUIDOT *et al.* 2011; LARRIEU and CABANETTES 2012; Fig. 3). In a study by RANIUS *et al.* (2009), less than 1 percent of the pedunculate oaks under 100 years of age had cavities, while 50 percent of the oaks between 200 and 300 years of age already had cavities and all of them had cavities at the age of 400 years. Only the thickest, oldest trees bear many different or all possible tree-related microhabitats (Fig. 3). The ecological value of a tree therefore increases with increasing age and diameter. If an old habitat tree with several TreMs is harvested, it takes decades or even centuries to replace it equivalently. This is why habitat trees are given more attention than previously in many European countries today. Among the initiatives for the protection of habitat trees, the Ancient Tree Forum based in England is worth mentioning: for more than 20 years, so-called “veteran trees” (a term used to designate particularly old, remarkable trees) have been inventoried with the help of the population throughout England in order to disseminate knowledge about them and promote their protection (www.ancienttreeforum.co.uk).

Besides age and diameter, the species identity of trees also influences the frequency and diversity of their TreMs. In general, deciduous trees form TreMs more frequently, more rapidly and at an earlier age than conifers (LARRIEU and CABANETTES 2012). For example, a comparison of beech (*Fagus sylvatica*) and silver fir (*Abies alba*) trees with a diameter of 25–50 cm shows that 43 percent of beech and only 9 percent of silver fir have TreMs (Table 1). Due to their physiognomy, with large branches that can die and break, deciduous trees tend to develop TreMs at a young age.

Certain TreMs are more common on deciduous trees – for example, water-filled concavities (dendrotelms) and cracks, whereas others are more common on coniferous trees (e.g. witches’ broom). Mixed stands therefore have a greater diversity of TreMs than pure

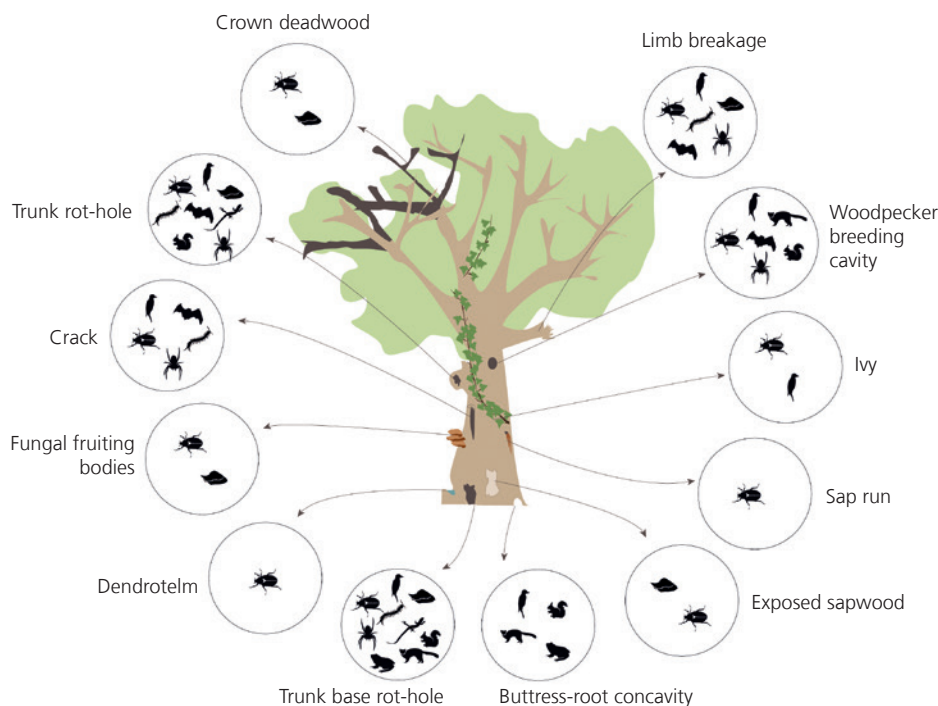


Fig. 2. A habitat tree carries various tree-related microhabitats, which serve as shelter, as well as breeding, wintering and feeding places, and are sometimes even necessary for the entire life cycle of the respective species (according to EMBERGER *et al.* 2016, modified).

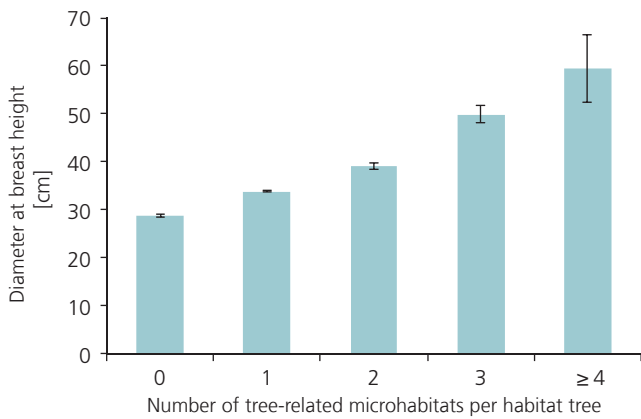


Fig. 3. Only the thickest trees bear many tree-related microhabitats. Mean values with standard error; all differences between classes are significant except for those between classes 3 and ≥ 4 . From BÜTLER and LACHAT 2009.

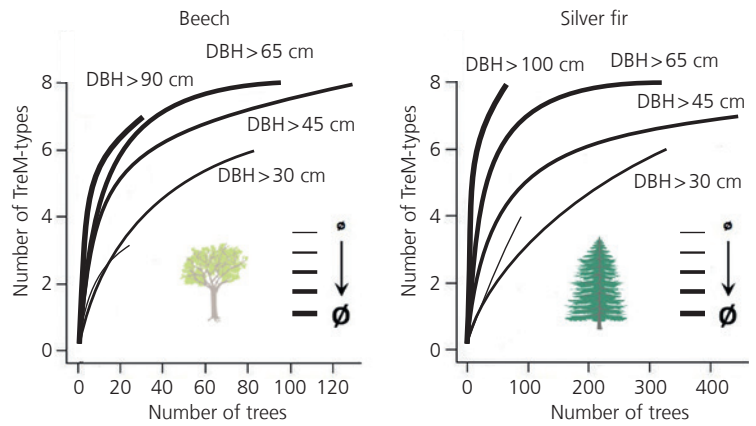


Fig. 4. The larger the trees, the fewer trees a stand needs to maintain the diversity of tree-related microhabitats. DBH: Diameter at breast height. Modified from LARRIEU *et al.* 2014.

stands, especially if the mixed stands also contain pioneer and secondary tree species such as birches or trembling poplars. Some of these species develop TreMs relatively quickly, for example cavities (LARRIEU *et al.* 2012).

Management influences the diversity, density and distribution of habitat trees

Naturally, the spatial density of tree-related microhabitats in forests is very high: according to studies in the Romanian and Ukrainian Carpathians and in the Dinaric Alps (COMMARMOT *et al.* 2013; KOZÁK *et al.* 2018), one in three or even one in two trees in natural forests supports microhabitats. In these mixed forests dominated by deciduous trees there was an average of more than 400 TreMs/ha. In Switzerland, 30 or more years ago unmanaged forests had 220 TreMs/ha, whereas recently (5–10 years ago) managed stands had 95 TreMs/ha (BÜTLER and LACHAT 2009). This ratio corresponds to the observations in German beech forests (WINTER and MÖLLER 2008). In an integratively managed beech-oak forest with regular interventions located in Steigerwald (Bavaria), 130 TreMs/ha were found, while 456 TreMs/ha were found in a neighbouring area that had not been managed for more than 40 years (KRAUS *et al.* 2017).

Managed forests generally have fewer TreMs than natural forests. In a study in deciduous forests in southwestern France, there was a frequency of 48

Tree-related microhabitats are ephemeral

The development stage of a tree-related microhabitat with rotting wood influences which species are present. To illustrate this, we take an oak tree which, after damage to the bark, has the underlying sapwood exposed. If the tree does not cover the injury, the injury will gradually develop into an increasingly voluminous mould rot-hole. During this development, several stages of wood decomposition will take place in a process that takes decades (cf. Merkblatt "Totholz im Wald. Entstehung, Bedeutung und Förderung"). Different species live during each stage of decomposition, as illustrated with the family of click beetles (Elateridae) in Fig. 5. Exposed sapwood (far left in the figure) by no means has the same physical-chemical and microclimatic properties as fully evolved rot-holes (far right in the figure).

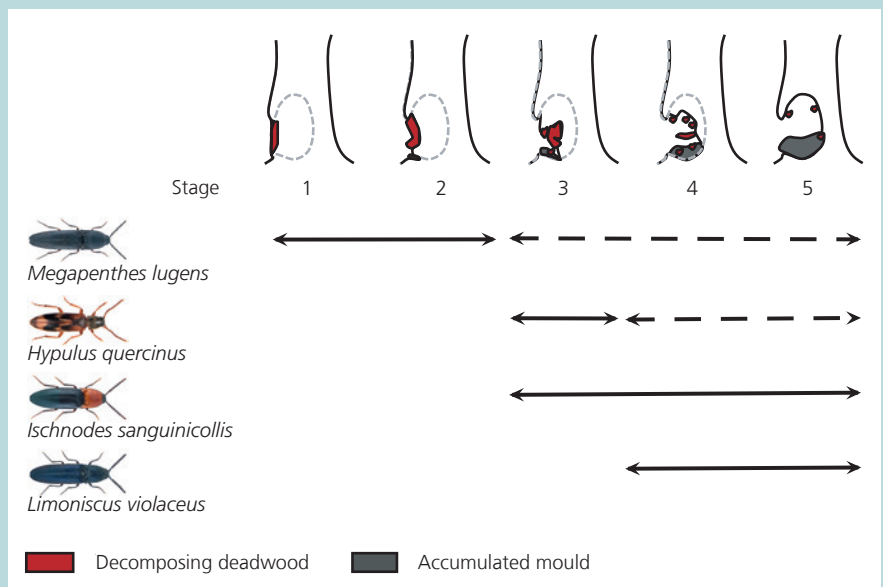


Fig. 5. Succession of click beetles (Elateridae) in the course of the development of a trunk base rot-hole with ground contact on an oak tree. The solid arrows show the stages preferred by the beetle species; the dotted arrows show where it is less common. Drawings: Nicolas Gouix.

Tab. 1. Proportion of trees by diameter class in natural forests bearing tree-related microhabitats. Beech (*Fagus sylvatica*) and silver fir (*Abies alba*). DBH: diameter at breast height. From LARRIEU and CABANETTES (2012).

Diameter class	Trees with tree-related microhabitats (%)	
	Beech	Silver fir
Small trees (20 ≤ DBH < 25 cm)	35	6
Medium trees (25 ≤ DBH < 50 cm)	43	9
Large trees (50 ≤ DBH < 70 cm)	78	21
Very large trees		
DBH ≥ 70 cm	92	32
DBH ≥ 89 cm	99	
DBH ≥ 99 cm		70

TreMs/ha immediately after logging, rising to 170 TreMs/ha after 70–80 years without silvicultural intervention (LARRIEU *et al.* 2017). The increase was even more spectacular for fungal fruiting bodies and woodpecker breeding cavities: in 70–80 years the number of fungal fruiting bodies increased from 1.5 to an average of 10.4 per hectare, and the number of woodpecker breeding cavities rose from 1.3 to 16.8 per hectare. Elsewhere in France, in mixed mountain forests of spruce, fir and beech, the spatial TreM density has doubled in 50 years of set-aside management (PAILLET *et al.* 2017).

Studies from Germany and Switzerland, among other countries, have shown that the number and diversity of TreMs in natural forests increases with the age of the trees (WINTER and MÖLLER 2008; BÜTLER and LACHAT 2009). In regularly managed forests, however, fewer TreMs are found on comparably old trees than in natural forests, because timber harvesting and silvicultural measures have a negative impact on the occurrence of TreMs (LASSAUCE *et al.* 2013; PAILLET *et al.* 2017). TreMs often cannot develop at all if weak, malgrown or already dead trees are removed prematurely from stands during thinning. This is especially the case for deciduous trees. At the same time, harvesting trees with a small target diameter leads to trees being removed before TreMs are formed. This mainly concerns conifers that naturally form TreMs late in their life (LARRIEU and CABANETTES 2012; LARRIEU *et al.* 2014). A good example of the effect of thinning strength is found in the northern Steigerwald (Bavaria), where it was found that in only slightly thinned areas

significantly more TreMs occurred, both in the stand as a whole and per tree, than in intensively thinned areas. One reason for this is the clear vitalisation of the trees released (MERGNER 2018). In forests that have not been subject to artificial selection for several decades, trees naturally form a large number of different TreMs as they grow older and thicker.

Besides their frequency, the diversity of TreMs within the forest stand and, at the same time, on each individual tree is crucial for the preservation of biodiversity. Here, too, there are considerable differences between natural and commercial forests. In Switzerland, only 5.1 percent of the trees in recently used forests bore at least two different TreMs, compared with 12.5 percent in stands that have been unmanaged for at least 30 years (BÜTLER and LACHAT 2009). On the other hand, certain TreMs are, on average, more common in commercial forests (VIDOT *et al.* 2011; LARRIEU *et al.* 2012). This is the case, for example, for exposed sapwood from injuries caused by felling or skidding and for dendrotelms, which often occur on stumps in former coppice or coppice with stand-ard forests.

Duration of development of tree-related microhabitats in natural forests

How long the development of tree-related microhabitats takes is highly variable: from a few milliseconds for the formation of a lightning scar to several decades for the formation of a large rot-hole. The duration during which a TreM is usable for an associated species also

varies widely (box “Tree-related microhabitats are ephemeral”). For example, a sap run that is active mainly in spring provides beetle larvae with a food source for only a few weeks, and a dendrotelm allows certain dipteran species to develop only as long as it contains water. On the other hand, a voluminous rot-hole can house specialised beetle populations for several decades. Moreover, since TreMs are by definition small and spatially separated from each other, either by their positions on the tree or by the distance between habitat trees, they are called ephemeral resource patches. As soon as a particular TreM disappears, the organisms associated with it must find a similar TreM within a distance accessible to them in order to survive.

Relatively little is known about the development rate of TreMs. In the mixed natural forests of the Pyrenees, TreMs develop on beech trees about twice as fast as on silver firs. Model calculations show natural rates of development of 0.82–1.28 TreMs/ha and year for beech and 0.5–0.9 TreMs/ha and year for fir (COURBAUD *et al.* 2017). In view of these low rates of occurrence, it takes about 100 years until a currently managed forest stand develops all TreMs potentially present in a natural forest. Therefore, the habitat trees already present in our forests today must be preserved and the development of future ones must be promoted (MERGNER 2018). Candidate habitat trees must be identified and preserved at an early age so that they can later develop into large habitat trees. Pioneer as well as secondary tree species with low economic value, which are most likely to form TreMs quickly, are also suitable for this purpose.

Need for a standardised methodology

Both in forest ecological research and in biodiversity-friendly forest management, habitat trees and thus the tree-related microhabitats they bear have gained increasing awareness in recent years. Until recently, TreMs and habitat trees were not uniformly assessed and measured. The definition of habitat trees and the criteria for their selection tend to vary depending on the study and inventory. Under the leadership of the European Forest Institute (EFI), experts

from all over Western and Central Europe have developed a TreM catalogue (KRAUS *et al.* 2016), which is now also available as a smartphone app (I + TreMs). Since then this catalogue has been further developed and published (LARRIEU *et al.* 2018). This publication is the basis for a standardised inventory method for TreMs and habitat trees, which is applicable in all temperate and Mediterranean European forests (Fig. 7).

A standardised method is also helpful for monitoring, forest certification and performance review of measures to promote biodiversity in forests, as adopted by the Swiss Federal Council in its Forest Policy 2020 and in the Swiss Biodiversity Strategy.

Hierarchical typology for different purposes

The typology of tree-related microhabitats proposed by LARRIEU *et al.* (2018) is organised in a hierarchical structure (Fig. 7). The first level consists of seven forms based on features relevant to biodiversity: (i) cavities in a broad sense, (ii) tree injuries and exposed wood, (iii) crown deadwood, (iv) excrescences, (v) fruiting bodies of saproxylic fungi and slime moulds, (vi) epiphytic, epixylic and parasitic structures, and (vii) exudates. These seven forms are further divided into 15 groups in a second level and 47 different types in a third level. Thanks to its hierarchical structure, the typology is useful for various purposes. For the quick selection of habitat trees when marking timber, the seven forms may be sufficient. For forest inventories or monitoring purposes, we recommend using either the 15 groups or the 47 types. In order to investigate the relationships between species and TreMs in forest ecological research, the 47 types can be further subdivided according to additional criteria (box “Tree-related microhabitats are complex structures”); see the field guide to tree-related microhabitats (BÜTLER *et al.* 2020). The field guide is available in the WSL Shop.

Data from different inventories can only be merged if the defined forms, groups and types and the proposed size limits are used exactly as outlined (Fig. 7). This is important for research, but also for monitoring and evaluating the success of subsidised measures to promote biodiversity. Some of the pro-

posed size limits are ecologically relevant, i.e. they influence the associated biodiversity. In cases where species-specific size limits were not available from the literature, they were set by experts in order to reduce the observer effect as much as possible.

Description of the seven tree-related microhabitat forms

Cavities are holes in the wood or sheltered places on the trunk or at the base of the trunk. They are caused by animals, such as woodpeckers, or insects living in the wood, by the decomposition processes of the wood, or by buttress roots. Thanks to the buffered microclimate inside, they provide shelter or a place to reproduce for many species. Woodpecker breeding cavities (Fig. 8a) play an important role for secondary users (birds, bats, and small mammals such as dormice and martens, but also invertebrates such as spiders, beetles and wasps). Depending on its location, from close to the ground and in contact with the soil to high on the trunk, a rot-hole (Fig. 8b) serves as a breeding site for specialised beetles or as a resting place for bats or other vertebrates, such as

birds, amphibians, lizards and mammals like the wildcat. With the accumulation of mould over time, a rot-hole becomes home to increasingly specialised species. Highly advanced rot-holes are vital for the severely endangered hermit beetle (*Osmoderma eremita*), for example. This rare beetle can only survive in this type of cavity, which it almost never leaves during its life. A dendrotelm is a concavity filled with water, often temporarily. Several species of insects and various micro-crustaceans are strictly dependent on dendrotelms. A total of 15 different cavity types are distinguished.

Tree injuries or exposed sap- or heartwood makes it easier for many primary colonisers to gain access to the wood. They occur either naturally, as a result of mechanical impacts such as trunk or crown breakage due to wind, ice or snow, but also due to lightning, frost or fire; they can also result from damage caused by felling trees in the vicinity or by timber transport. If the tree does not cover its wound, the exposed wood can slowly develop into a rot-hole. Exposed heartwood and sapwood resulting from the breaking of a crown or main branch provides transition condi-

Tree-related microhabitats are complex structures

Perennial fungal fruiting bodies are clearly delimited habitats (Fig. 6). However, they usually contain different beetle communities, each of which uses only a very specific part of the fungus. For example, on the hoof fungus (*Fomes fomentarius*) fruiting body, the rodent beetle *Dorcatoma robusta* and the black beetle *Bolitophagus reticulatus* feed on the trama, the dwarf beetle *Pteryx suturalis* on the spores in the tubes, and the flat bark beetle *Peltis grossa* and the scarab beetle *Melandrya dubia* on the mycelium between the fruiting body and the tree trunk (Bouget pers. comm.). Each tree-related microhabitat (TreM) is therefore in reality a mosaic of smaller habitats. Nevertheless, for practical reasons, the whole fungal fruiting body is regarded as one TreM. The fungal species identity, the size of the fungal fruiting body, and its stage of development influence the composition of the associated species communities (THUNES and WILLASSEN 1997).



Fig. 6. Red-banded polypore (*Fomitopsis pinicola*), an apparently clearly defined habitat (left) and cross-section of a hoof fungus (*Fomes fomentarius*) fruiting body (right).

















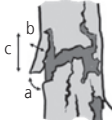



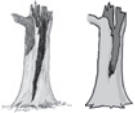

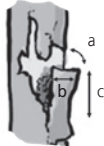



Form	Cavities				Tree injuries and exposed wood		Crown deadwood
Group	Woodpecker breeding cavities	Rot-holes	Insect galleries	Concavities	Exposed sapwood only	Exposed sapwood and heartwood	Crown deadwood
Type	Small breeding cavity $\varnothing < 4$ cm 	Trunk base rot-hole (closed top, ground contact) $\varnothing > 10$ cm 	Insect galleries and bore holes $\varnothing > 2$ cm or $\square > 300$ cm ² 	Dendrotelm or water-filled concavity $\varnothing > 15$ cm 	Bark loss $\square > 300$ cm ² 	Stem breakage Stem \varnothing at breakage > 20 cm 	Dead branches $\varnothing > 10$ cm or $\varnothing > 3$ cm plus $> 10\%$ of the crown is dead 
	Medium-sized breeding cavity $\varnothing = 4-7$ cm 	Trunk rot-hole (closed top, no ground contact) $\varnothing > 10$ cm 		Woodpecker foraging excavation $\Downarrow > 10$ cm, $\varnothing > 10$ cm 	Fire scar $\square > 600$ cm ² 	Limb breakage (heartwood exposed) $\square > 300$ cm ² 	Dead top $\varnothing > 10$ cm at the base 
	Large breeding cavity $\varnothing > 10$ cm 	Semi-open trunk rot-hole $\varnothing > 30$ cm 		Bark-lined trunk concavity $\Downarrow > 10$ cm, $\varnothing > 10$ cm 	Bark shelter (open at the bottom) $a > 1$ cm, $b > 10$ cm, $c > 10$ cm 	Crack Length > 30 cm, width > 1 cm, $\Downarrow > 10$ cm 	Remnants of a broken limb Branch $\varnothing > 20$ cm, stub length > 50 cm 
	Woodpecker "flute" (breeding cavity string) ≥ 3 cavities aligned $\varnothing > 3$ cm 	Chimney trunk rot-hole with/without ground contact $\varnothing > 30$ cm 		Buttress-root concavity $\varnothing > 10$ cm Roof inclination $< 45^\circ$ 	Bark pocket (open at the top) $a > 1$ cm, $b > 10$ cm, $c > 10$ cm 	Lightning scar Length > 30 cm, width > 1 cm, $\Downarrow > 10$ cm 	
	Hollow branch $\varnothing > 10$ cm 				Fork split at the intersection Length > 30 cm 		

Fig. 7. Recommended typology of tree-related microhabitats according to LARRIEU *et al.* (2018), divided into 7 forms, 15 groups and 47 types. The recording thresholds should be followed for all recordings to allow comparison of the data regardless of the hierarchical level used (forms, groups or types). \varnothing = diameter; \Downarrow = depth; \square = area. Drawings: C. Emberger, L. Apfelmacher/D. Kraus and reproductions from KRAUS *et al.* 2016

tions for organisms between living and dead wood. Cracks, shelters and pockets in the bark are particularly important for the daytime resting, breeding and wintering of some bats and as nesting places for birds, bugs and spiders. A total of nine TreM types can be distinguished in this form.

Thanks to its sun-exposed location, **crown deadwood** offers dry, warm conditions that are often rare in our closed forests. In addition to dead branches, stem and limb breakage belong to this form.







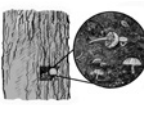






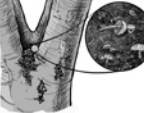






Excrescences, i.e. cankers, burrs and witches' brooms, are often caused by reactive growth of the tree after a para-

sitic or microbial attack to isolate the pathogen. In addition to the three types mentioned above, this form of tree-related microhabitat also includes epicormic shoots, which are either genetically determined or can form as a result of suddenly increased exposure of the trunk to light.

Fungal fruiting bodies are reproductive organs of fungi. A distinction is made between ephemeral fruiting bodies present visible for less than a year and perennial fruiting bodies lasting several years. The fruiting bodies of saproxylic fungi dependent on old trees and dead wood indicate a high diversity of fungal species, but also favour other forest spe-

cies such as beetles, flies, bees, butterflies and bugs. A total of five TreM types belong to this form (including the slime fungi or so-called myxomycetes).

Epiphytic and epixylic structures include various tree-related microhabitats for which the tree serves mainly as a physical support. These include mosses, lichens, ferns and mistletoe as well as nests of vertebrates and invertebrates. Also worth mentioning are the so-called microsoils, which form either in chapped bark or on the flat parts of fork trees of organic material such as rotting leaves, bark and mosses. Nine types of TreMs belong to this form.

Excrescences		Fruiting bodies of saproxylic fungi and slime moulds		Epiphytic and epixylic structures			Exudates
Twig tangles	Burrs and cankers	Perennial fungal fruiting bodies	Ephemeral fungal fruiting bodies and slime moulds	Epiphytic and parasitic crypto- and phanerogams	Nests	Microsoils	Fresh exudates
Witches' broom ø > 50 cm 	Burr ø > 20 cm 	Perennial polypore ø > 5 cm 	Annual polypore ø > 5 cm or group of > 10 	Bryophytes □ > 10% of the trunk is covered 	Vertebrate nest ø > 10 cm 	Bark microsoil 	Sap run Length > 10 cm 
Epicormic shoots > 5 shoots 	Canker ø > 20 cm or covering a large part of the trunk 		Pulpy agaric ø > 5 cm or group of > 10 sporophores 	Foliose and fruticose lichens □ > 10% of the trunk is covered 	Invertebrate nest 	Crown microsoil 	Heavy resinosis Length > 10 cm 
			Large pyrenomyces ø > 3 cm or group covering > 100 cm ² 	Ivy or lianas □ > 10% of the trunk is covered 			
			Myxomycetes (slime moulds) ø > 5 cm 	Ferns > 5 fronds 			
				Mistletoe ø > 20 cm 			

Download the tree-related microhabitat typology enlarged as PDF



Exudates are either active sap runs or heavy resinosis. Beetles, flies and butterflies are the main beneficiaries of sap runs.

How are habitat trees recorded?

Tree-related microhabitats are often small. For example, it is difficult to discover a lesser spotted woodpecker breeding cavity at a height of 20 metres with the naked eye. We therefore recommend working with binoculars. In addition, recordings performed when the trees are leafless are easier and more

accurate. Subjective perception also plays an important role in the accuracy of TreM recordings (PAILLET *et al.* 2015). Therefore, clear instructions and a simple and unambiguous method are essential. Ideally, the recordings are made in teams of two, although an experienced person can also make complete recordings alone. Each tree is inspected from the base of the trunk to the crown. It is best to go around the tree once for the lower part of the trunk and a second time, at a greater distance, for the upper part and the crown. A careful observation of a tree requires between one and three minutes, depending on the size of the tree, number of TreMs, slope and level

of detail of the inventory. The minimum tree diameter must be determined appropriately. For research and monitoring purposes we recommend a caliper limit of about 10–20 cm. In the context of routine forest inventories, it is advisable to adapt this limit to the usual threshold. For financial incentives, the quality criteria and minimum diameters defined by the authorities apply.

Habitat tree recordings with a smartphone

The localisation, identification and inventory of habitat trees is a challenge. A recently developed smartphone appli-



Fig. 8. (a) This pedunculate oak shows that woodpeckers sometimes drill their cavities into the same tree for several years. Abandoned woodpecker cavities can serve secondary users such as birds, bats, rodents, spiders and wasps. (b) It takes many decades for a voluminous rot-hole to form. It is one of the rarest tree-related microhabitats in commercial forests. This tree-related microhabitat is essential for certain highly specialised beetle species. For this reason, special attention should be paid to the conservation of rot-holes.

ation facilitates the task (HabiApp, Fig. 9). This application is available free of charge. The app enables the localisation of habitat trees via GPS, the standardised recording of their characteristics (tree species, diameter) and the taking of photos. The inventory of TreMs is based on the typology of LARRIEU *et al.* (2018). The recorded data can be used, for example, for forest planning or monitoring purposes. Furthermore, they can help to assess the ecological forest infrastructure on different spatial scales: local (stand), regional or even national.

How many habitat trees should be preserved?

The greater the density of habitat trees in a forest stand, the better the associated biodiversity is promoted. However, in commercial forests a compromise must be reached between timber production and the preservation of biodiversity. In addition to the forest type, the forest stand age, the management intensity and the possible presence of rare, specialised species must be taken into

account. In a forest area with intensive timber production and only a few protected forest areas and old-growth forest islands, more habitat trees are needed to mitigate the effects of timber use on organisms dependent on tree-related microhabitats. In addition, species

that are highly specialised or have limited mobility require a higher habitat tree density than highly mobile, generalist species.

A TreM is always ephemeral (see box “Tree-related microhabitats are ephemeral”). It can disappear for three reasons:

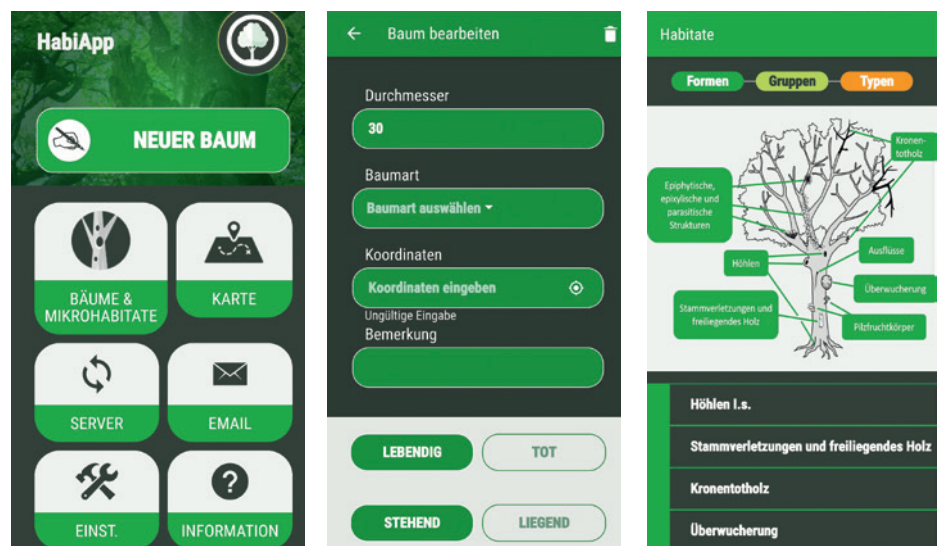


Fig. 9. Application for recording habitat trees with a smartphone.

(i) when the tree is harvested or naturally falls down; (ii) through its natural evolution towards another TreM type, for example, the transition from an injury to a rot-hole over time or shifts associated with the altered microclimatic conditions following the death of the habitat tree; and (iii) when the TreM is temporarily unavailable to organisms, such as a dendrotelm that dries out during a period without rain. Consequently, repeated selection of habitat trees is essential. In addition, TreMs must be numerous and spatially distributed enough to be accessible to their associated taxa. There is still little information in the scientific literature on the spatial distribution of TreMs and their temporal dynamics. Nevertheless, there are some recommendations for the minimum spatial density of habitat trees in commercial forests, ranging from 5 to more than 10 trees per hectare (SCHEIDEGGER and STOFER 2015; BÜTLER *et al.* 2013; WINTER *et al.* 2016; MERGNER 2018).

A recommended management strategy for the promotion of TreM-associated biodiversity combines two complementary approaches: (i) the creation of protected forest areas and old-growth forest islands without intervention, thus maintaining natural processes, and (ii) the preservation of habitat trees in the entire commercial forest area. Unmanaged forest areas result in a high spatial density of TreMs, which is difficult to achieve in commercial forests despite integrative approaches with close-to-nature management (PAILLET *et al.* 2017;

MERGNER 2018). A proportion of about 10–20 percent of the forest area devoted to natural dynamics seems to be necessary to largely preserve the diversity of forest species (LARRIEU *et al.* 2012; BOUGET and PARMAN 2016). According to LARRIEU *et al.* (2014), areas in beech-fir mixed forests dedicated to natural dynamics should be at least 10 hectares (ideally >20 hectares) in order to achieve and maintain the full diversity of TreMs in the long term.

Target values and guidelines

The target values in the guidelines of the forestry services or national offices are well below the threshold values formulated by scientists, as they are the result of compromises in the negotiation processes of forest policy. It is uncertain, however, whether the achievement of these target values will actually preserve TreM-dependent species.

In Switzerland, the Federal Office for the Environment FOEN has defined a national target of three to five habitat trees per hectare of forest area by 2030, combined with 2–3 percent old-growth forest islands and 5 percent protected forest areas without silvicultural intervention (IMESCH *et al.* 2015). Baden-Württemberg (Germany) is aiming for the permanent retention of one habitat tree group – approximately 15 predominant and co-dominant trees – per three hectares of state forest (ForstBW 2015 and 2016). With this goal, a theoretical average distance of about 170 metres be-

tween the individual habitat tree groups is achieved. In the long term, the Bavarian State Forests want to achieve a density of 10 habitat trees per hectare in all semi-natural stands of a certain age (Bayerische Staatsforsten AÖR 2009). A particularly biodiversity-friendly concept has been implemented in the Steigerwald in northern Bavaria on 17,000 hectares of forest: it comprises the preservation of 10 habitat trees per hectare as well as 210 old-growth forest islands between 0.3 and 20 hectares in size as stepping stones between the 6 nature forest reserves (Bayerische Staatsforsten AÖR 2017). This concept is proving successful and has contributed to increasing local forest biodiversity. For example, the black beetle *Bolitophagus reticulatus*, a species living in the fruiting bodies of the fungus *Fomes fomentarius*, which is very rare in Switzerland and threatened throughout Bavaria, has spread throughout the Steigerwald (ZYTYSKA *et al.* 2018).

Other German federal states such as Hesse or Rhineland-Palatinate and several Swiss cantons also have concepts for the retention of old trees and dead wood, including the promotion of habitat trees. In France, the Office National des Forêts ONF, the administration for public forests, has issued standards that are mandatory for state forests and recommended for other communal forests: at least two cavity trees and at least one snag or dying tree per hectare (ONF 2009). In private forests, only owners who are members of the PEFC



Fig. 10. Habitat trees in commercial forests are increasingly marked to ensure their long-term preservation. Canton Vaud (a), French state forests (b), Bavaria (c).

or FSC certification labels undertake to maintain at least one old or large tree or cavity tree per hectare (PEFC 2016) and at least two habitat trees (according to a list of 12 TreM types), with the aim of securing five habitat trees per hectare by the end of the forest management plan's term (FSC 2017). Such concepts also cover other aspects important to forest managers, such as the safety or marking of habitat trees in the forest.

In summary, any efforts to preserve and promote habitat trees through appropriate silvicultural practices contrib-

ute to increasing the biodiversity of forest stands. Biodiversity provides various ecological services that are increasingly valued by society and contributes to increasing the resilience and adaptability of forests to disturbances.

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Recommendations for practice

The conservation and promotion of habitat trees should be an integral part of all forestry activities, such as silvicultural care, thinning and logging. Consequently, specific information on the selection, number and distribution of habitat trees should be included in the operational guidelines of forest enterprises.

Recommendations for forest planning:

- Designate **set-aside areas**, dedicated to natural dynamics, where trees can age and complete their entire life cycle. Natural forest reserves and old-growth forest islands are two instruments that are also suitable for the conservation of habitat trees in high spatial density. Such areas should be permanently retained in order to have all forest development phases represented. Old-growth forest islands are useful as stepping stones between larger protected areas and should be larger than 10 hectares whenever possible.
- For a functional network of typical natural forest structures, in addition to the areas without intervention, **managed stands should include many habitat trees**.
- **Promote mixed stands with secondary tree species**, as the different tree species have different tree-related microhabitats. In general, short-lived pioneer tree species quickly form TreMs and contribute greatly to their diversity.
- For each silvicultural intervention, its impact on tree-related microhabitats must be assessed and the **habitat tree candidates** must be identified, i.e. trees with the potential to bear TreMs in the future. By positive selection of the value-trees (elite trees), habitat trees are preserved, as there is no reason to remove them due to their low economic value. Habitat tree candidates should be left in young forest stands from the thinning onwards and marked. Due to the negative selection of vital trees with undesirable gross malformation, which was common in the past in the care of young growth, the development of TreMs was often limited (MERGNER 2018; WINTER *et al.* 2016).

Recommendations in the forest stand:

- In managed stands, aim for a minimum of **six to ten habitat trees per hectare** to mitigate the impact of forestry on organisms dependent on tree-related microhabitats.

- When selecting habitat trees, **focus on TreM-bearing, old or large trees**. Trees that bear TreMs at an early age will most likely develop more TreMs as they get older. In general, the diameter correlates positively with the number of TreMs and the largest trees have the greatest variety of TreMs. As a rule, all possible types of TreMs can be obtained by selecting habitat trees with diameters > 50 cm for beech and > 65 cm for silver fir (LARRIEU *et al.* 2014). From a diameter of about 90 cm (beech) or 100 cm (silver fir), trees bear significantly more TreMs than thinner trees (LARRIEU and CABANETTES 2012).
- **Preserve also pioneer and co-dominant secondary tree species**, as they rapidly develop TreMs.
- Aim for a **combination of grouped and scattered habitat trees**.
- Preserve various TreMs, with **special attention to the rarest ones** (fungal fruiting bodies on living trees, cracks and sap runs) and those with particularly long developmental periods (e.g. large rot-holes).
- Pay special attention to **habitat trees at forest edges** and along linear structures such as streams and pond or lake shores, as certain TreMs such as sap runs or cracks are more common there than in the interior of the forest.
- Preserve also snags, as they carry on average more TreMs than living trees (VUIDOT *et al.* 2011) and provide a large proportion of certain TreMs, especially fungal fruiting bodies and cracks (LARRIEU and CABANETTES 2012).
- For habitat tree recordings use the **typology of LARRIEU *et al.* (2018)** (Fig. 7), with the respective size limits. Depending on the objective, 7 forms, 15 groups or 47 types of TreMs can be used.
- **Mark habitat trees in the field** (Fig. 10) and record their coordinates and other characteristics (diameter, tree species, TreMs) in order to secure and preserve them in the long term. This will also enable future local decision-makers to take these habitat trees into account in forest planning.

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Images

Rita Bütler (Fig. 1, 6 left, 8, 10a), Laurent Larrieu (Fig. 6 right), Yoan Paillet (Fig. 10b), Daniel Kraus (Fig. 10c).

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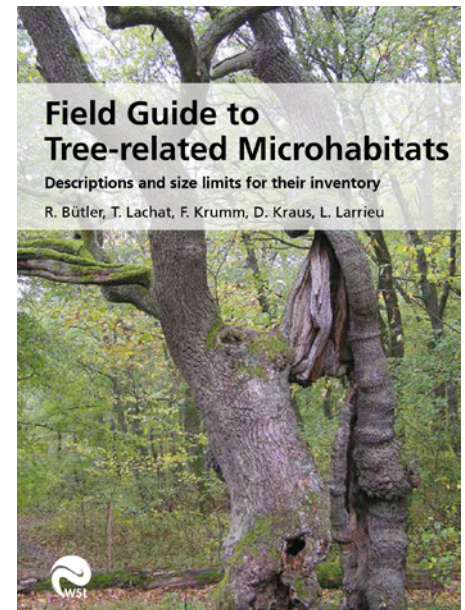
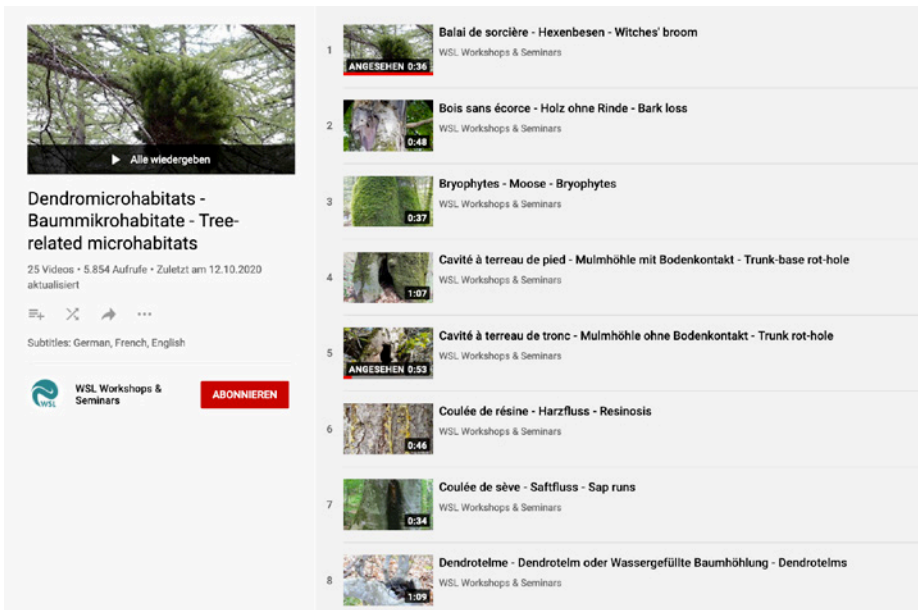
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Short videos on YouTube about tree-related microhabitats

You can see tree-related microhabitats on trees and get information from an expert by watching our short videos with subtitles in English.



For additional information on the frequency of occurrence and stand replacement rate for the 47 types of tree-related microhabitats.



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