



HAL
open science

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

Laurent Larrieu, Benoit Courbaud, Christophe Drénou, Goulard Michel, Rita Bütler, Daniel Kozák, Daniel Kraus, Frank Krumm, Thibault Lachat, Jörg Müller, et al.

► To cite this version:

Laurent Larrieu, Benoit Courbaud, Christophe Drénou, Goulard Michel, Rita Bütler, et al.. Key factors determining the presence of Tree-related Microhabitats: A synthesis of potential factors at site, stand and tree scales, with perspectives for further research. *Forest Ecology and Management*, 2022, 515, 10.1016/j.foreco.2022.120235 . hal-03703501

HAL Id: hal-03703501

<https://hal.inrae.fr/hal-03703501>

Submitted on 22 Jul 2024

HAL is a multi-disciplinary open access archive for the deposit and dissemination of scientific research documents, whether they are published or not. The documents may come from teaching and research institutions in France or abroad, or from public or private research centers.

L'archive ouverte pluridisciplinaire **HAL**, est destinée au dépôt et à la diffusion de documents scientifiques de niveau recherche, publiés ou non, émanant des établissements d'enseignement et de recherche français ou étrangers, des laboratoires publics ou privés.



Distributed under a Creative Commons Attribution - NonCommercial 4.0 International License

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

3 Shortened title version: Key factors for Tree-related Microhabitats

4 **Authors**

5 Laurent **Larrieu**^{a,b,*}, Benoit **Courbaud**^c, Christophe **Drénou**^d, Michel **Goulard**^a, Rita **Bütler**^e, Daniel
6 **Kozák**^f, Daniel **Kraus**^g, Frank **Krumm**^h, Thibault **Lachat**^{i,h}, Jörg **Müller**^{j,k}, Yoan **Paillet**^c, Andreas **Schuck**^l,
7 Jonas **Stillhard**^h, Miroslav **Svoboda**^f, Kris **Vandekerkhove**^m

8

9 (In bold : family names)

10 * Corresponding author ; laurent.larrieu@inrae.fr; +33601082264

11

12 ^a Université de Toulouse, INRAE, UMR DYNAFOR, Castanet-Tolosan, France ; laurent.larrieu@inrae.fr
13 ; michel.goulard@inrae.fr

14 ^b CNPF-CRPF Occitanie, France

15 ^c University Grenoble Alpes, INRAE, UR LESSEM, France ; benoit.courbaud@inrae.fr,

16 yoan.paillet@inrae.fr

17 ^d CNPF-IDF, Toulouse, France ; christophe.drenou@cnpf.fr

18 ^e Swiss Federal Research Institute WSL & Plant Ecology Research Laboratory, School of Architecture,
19 Civil and Environmental Engineering, Ecole Polytechnique Fédérale de Lausanne, Switzerland;

20 rita.buetler@wsl.ch

21 ^f Czech University of Life Sciences, Faculty of Forestry and Wood Sciences, Czech Republic;

22 kozakdaniel12@gmail.com; svobodam@fld.czu.cz

23 ^g Bayerische Staatsforsten AÖR, Forstbetrieb Neureichenau, Dreisesselstraße 15, 94089

24 Neureichenau; Institute for Silviculture, Freiburg University of Freiburg, Tennenbacherstr. 4, 79085

25 Freiburg im Breisgau; daniel.kraus@baysf.de

26 ^h Swiss Federal Research Institute WSL, Birmensdorf; frank.krumm@wsl.ch, jonas.stillhard@wsl.ch

27 ⁱ Bern University of Applied Sciences, School of Agricultural, Forest and Food Sciences HAFL,

28 Zollikofen; thibault.lachat@bfh.ch

29 ^j Bavarian Forest National Park; joerg.mueller@npv-bw.bayern.de

30 ^k Department of Animal Ecology and Tropical Biology, University of Würzburg

31 ^l European Forest Institute, andreas.schuck@efi.int

32 ^m INBO, research team Forest Ecology and Management, Gaverstraat 4, 9500 Geraardsbergen;

33 Belgium; kris.vandekerkhove@inbo.be

34

35 **Author contribution statement**

36 LL, BC and CD designed the general structure of the manuscript. MG run statistical analysis. RB, DKo,

37 DKr, FK, TL, JM, YP, AS, JS, MS, KV contributed to discussion of the results and the writing of the final

38 document.

39

40 **Highlights**

- 41
- 42 • Plot context primarily explains tree-related microhabitats occurrence
 - 43 • Plot context is a black box combining environmental, management and biotic factors
 - 44 • From the literature, we identified 31 factors that may play a key role in TreM formation
 - 45 • A sub-set of 9 factors that should be prioritised in the future is suggested

46
47
48
49
50
51
52
53
54
55
56
57
58
59
60
61
62
63
64
65
66
67
68
69
70
71

Abstract

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

Keywords: TreMs; biodiversity conservation; Habitat trees; Integrative forest management; Key factors; Forest-dwelling taxa

72

73 **Introduction**

74 A Tree-related Microhabitat (TreM) is defined as “a distinct, well-delineated structure occurring on
75 living or standing dead trees, that constitutes a particular and essential substrate or life site for
76 species or species communities during at least a part of their life cycle to develop, feed, shelter or
77 breed” (Larrieu et al. 2018). TreMs support a wide array of biodiversity (see Table 2 in Larrieu et al.
78 2018) that is not usually supported by other forest structures, such as deadwood items (Stokland et
79 al. 2012). Several studies have highlighted the significant impact of an increase in TreM-bearing tree
80 (hereafter called habitat-tree) density on species richness for several taxa (see e.g. Bouget et al.
81 2013, 2014, Larrieu et al. 2019, and Winter and Möller 2008 for saproxylic beetles; Regnery et al.
82 2013a and Paillet et al. 2018 for bats and birds; Larrieu et al. 2019 for polypores and hoverflies; Basile
83 et al. 2020 for insects and bats). Hence, some authors have suggested using TreMs as indirect
84 biodiversity indicators in forest ecosystems and as tools to promote integrative forest management
85 (Kraus and Krumm, 2013; Winter and Möller 2008, Regnery et al. 2013b, Paillet et al. 2018; Bütler et
86 al. 2013; Larrieu et al. 2018; Asbeck et al. 2021). However, at plot and stand scales, the relationship
87 between TreM density and/or diversity with variations in biodiversity are not so straightforward.
88 Indeed, this relationship is only partially consistent, for both species’ richness and composition, when
89 considering a range of forest contexts (Bouget et al. 2013, 2014; Paillet et al. 2018). This is likely due
90 to complex interactions between TreMs and other resources (e.g. deadwood items, flowering plants
91 in clearings, water bodies; Larrieu 2014a), flaws in procedures for assessing taxa and TreMs (Larrieu
92 and Bouget 2017), time lags in the response of certain TreM-dwelling species to TreM presence
93 (Herrault et al. 2016), as well as the spatial distribution of source populations (Komonen and Müller
94 2018).

95 The spatial distribution of TreMs is not solely dependent on that of the TreM-bearing trees. Indeed,
96 they are typically limited in availability, persisting from only a few days for lignicolous agarics, to
97 several decades for large rot-holes. Thus, TreMs can be considered as Ephemeral Resource Patches

98 (ERP, Finn 2001). Furthermore, some of these structures are generated by stochastic events that
99 occur very rarely (e.g. lightning scars), or have a very long development time (e.g. fully evolved rot
100 holes). Numerous forest-dwelling species are continuity-dependent and therefore are restricted by
101 both development time of a novel habitat and the time required to colonize that novel resource
102 patch (Nordén et al. 2014). As a result, it is challenging to manage forests to ensure a continuous
103 resource supply for TreM-dwelling taxa. To provide forest managers with practical recommendations
104 for the conservation of TreM-dwelling taxa, i.e. which trees should be exempt from harvesting,
105 numerous studies have attempted to identify key features at the tree level that are linked to TreM
106 formation. They have highlighted the key roles of tree species, tree diameter at breast height (dbh)
107 and status (i.e. living vs standing dead) for driving the occurrence and abundance of TreMs (Winter
108 and Möller 2008; Michel and Winter 2009; Vuidot et al. 2011; Regnery et al. 2013b; Larrieu and
109 Cabanettes 2012; Larrieu et al. 2014b; Paillet et al. 2018, 2019; Kozák et al. 2018; Asbeck et al. 2019).
110 Notwithstanding the abundance of studies on the topic, to date, predictive models have mainly
111 focused on only two basic tree features, namely dbh and species for living trees (Courbaud et al.
112 2017; Jahed et al. 2020); in some cases, a qualitative variable was used to separate managed and
113 unmanaged forests (Courbaud et al. 2021). Dbh and tree-species are easy to record, and are also
114 routinely assessed by forest managers for silvicultural and monitoring purposes. However, the power
115 to predict TreM occurrence with these two tree features alone is often rather low, e.g. about 26 % in
116 beech (*Fagus sylvatica*)-silver fir (*Abies alba*) forests (Larrieu et al. 2014b). Moreover, Courbaud et al.
117 (2021) have shown that site effects are huge. However, these previous works have not been able to
118 highlight what site features influence the presence and dynamics of TreMs.

119 For these reasons, the distribution of TreMs is currently difficult to predict, hampering the
120 elaboration of appropriate management guidelines that take into consideration these crucial
121 biodiversity features. This is particularly important as the need to take TreMs into account in
122 silvicultural planning is increasingly acknowledged among forest managers. For example, TreMs have
123 been incorporated into an index that is routinely used in the field by forest managers in France (Index

124 of Biodiversity Potential, IBP; Larrieu and Gonin 2008; Gosselin and Larrieu 2020). At a larger spatial
125 scale, a rapidly growing network of about 160 training plots (called “marteloscopes”) has been
126 established across 22 countries, mainly in Europe, with the aim of improving managers’ knowledge
127 about TreMs and inventory calibration, employing tree-marking exercises in the field (Kraus et al.
128 2021). Therefore, there is a critical need to better explain and predict TreM occurrence and the
129 processes that lead to their formation, with the ultimate aim of encouraging forest managers to take
130 TreM-associated biodiversity into account in their daily work routines.

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

135 Plot context is currently a “black box” which combines local environmental conditions, past and
136 current management legacies, and local biotic features which might impact TreM formation in
137 several ways. Environmental conditions determine tree species assemblages in relation to both
138 biogeographic and bioclimatic contexts, as well as soil fertility. Soil fertility may determine the
139 presence of epiphytic plants that are considered as TreMs when they climb on trunks. For example,
140 ivy (*Hedera helix*) does not thrive on very acidic and nutrient-poor soils (Dumé et al. 2018). Thin soils
141 which are prone to be often dry can promote dead wood in the crown of the trees (Breda et al.
142 2004). Furthermore, the dynamics of TreM formation has been shown to differ between tree species
143 (Courbaud et al. 2017; Jahed et al. 2020) and not all tree species are likely to support the same type
144 of TreMs (Vuidot et al. 2011; Larrieu and Cabanettes 2012; Paillet et al. 2019). The presence of
145 particular geological features, such as cliffs or mobile scree, may increase the density of trees that
146 have bark loss or broken stems due to falling rock (Dorren and Berger 2006; Stokes et al. 2005). For
147 example, in the Black Forest (Germany), Asbeck et al. (2019) highlighted that increasing altitude
148 favours the number of buttress-root concavities and epiphytic lichens, while mosses and mistletoe
149 are more abundant at lower altitudes. However, the detailed effect of local conditions has, to date,

150 not yet been well quantified. Furthermore, such observations may actually mask confounding effects,
151 e.g. when altitude and slope are strongly and positively correlated, as is often the case in mountain
152 areas. Forest management is known to influence both the density and the diversity of TreMs (e.g.
153 Winter and Möller 2008; Larrieu and Cabanettes 2012), while the impact of harvesting persists over
154 the long term (Bouget et al. 2014; Paillet et al. 2015; Larrieu et al. 2016). In addition, certain biotic
155 features may have an effect on the presence and abundance of TreMs, e.g. density of red deer
156 (*Cervus elaphus*) in relation to food resource availability for bark loss (Verheyden et al. 2006), or the
157 presence of black woodpecker (*Dryocopus martius*) for both breeding holes and feeding concavities
158 (Bobiec et al. 2005).

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

166 Thirdly, based on a consideration of the trade-off between sampling effort and relevance for
167 explaining the occurrence of TreMs, evaluated from both literature and based on our own expertise,
168 we suggest a sub-set of features that i/ should be tested by further studies focusing on TreMs when
169 widely available (e.g. via large scale databases), or ii/ should be recorded in the future by researchers
170 in the field.

171

172 **Material and methods**

173 *Predictive power of the features currently available in most TreM datasets*

174 To quantify the predictive power of the features shared by most of the datasets, we used an
175 international database which integrates 23 harmonized datasets, comprising 100,855 living trees and

176 10,354 standing dead trees belonging to 89 tree species (appendix; Table 1SM). For each of the
177 eleven TreM subgroups that were designated by Courbaud et al. (2021), we built a Generalized
178 Linear Mixed Model (GLMM) that described the presence/absence of this TreM group in relation to
179 dbh, tree species, tree status (living/standing dead), plot context, and time since the last harvest
180 (four categories: <20y, 21-50y, 51-100y and >100y). Three two-way interactions - namely dbh with
181 status, dbh with time since last harvest, status with time since last harvest - were also included as
182 fixed effects. Interactions of plot context and tree species with dbh and status were included as
183 random effects. The interaction between plot context and tree-species was considered as redundant
184 and was not included in the models. We then simplified each full model by excluding each
185 explanatory factor in turn to quantify its effects in terms of the proportion of variance explained: plot
186 context, dbh, tree species, tree status and time since last harvest. The GLMM models were fitted
187 with a Bernoulli structure (binomial distribution and logit link) to describe presence/absence using
188 the BRMS Package (Bürkner 2021). The model took into account potential correlation among random
189 effects, with an a priori of no correlation. The a priori distributions were taken as normal $N(0,2)$ for
190 fixed effects, exponential with parameter equal to 1 for variances and the LKJ distribution for
191 correlation matrices, as recommended by McElreath (2020). We used BRMS for the analysis rather
192 than MCMCglmm since it uses the Stan library (Bürkner 2021) and therefore employs the
193 Hamiltonian MCMC that provides a better exploration of the posterior distribution, generating
194 results that are more robust with a shorter computational time. Note, however, that we also
195 analysed the same set of models using the MCMCglmm approach (Hadfield 2010) and obtained very
196 similar results. For BRMS, 1,000 iterations for the burn in, 2,000 iterations for the estimations with 4
197 chains in parallel were enough to obtain convergence compared to 200,000 iterations for burn in,
198 400,000 iterations for estimation with thinning of 100 for the MCMCglmm. Since plot context and
199 time since last harvest are mechanistically linked to tree dbh and to the presence/absence of certain
200 TreM groups, models that omitted these two variables were simply considered as a control.

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

204

205 *Assessing additional features that may play a key role in TreM formation*

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

218

219 **Results**

220 *Predictive power of the features currently available in the databases*

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

224

225 Table 1

226

227 *Additional features that may play a key role in TreM formation*

228 From the literature, we identified 21 features which may play an important role in TreM formation:
229 nine environmental site specific , two stand dependent and ten tree-related features (Table 2). The
230 feature implicated in the formation of the highest number of TreMs is the ontogenic stage of the
231 tree, potentially linked to eight TreMs. The TreM groups that were the most likely to be impacted
232 were *exposed sapwood and heartwood* (potentially linked to 10 factors), *epiphytic and parasitic*
233 *crypto- and phanerogams* (6 factors), *crown deadwood* (5 factors), *rot holes* (5 factors) and
234 *concavities* (4 factors).

235

236 Table 2

237

238 **Discussion**

239

240 **Features that may play a key role in TreM formation based on biological processes**

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

253 since compartmentalization capacity (Smith 2015) decreases with developmental stage (Table 2). The
254 establishment of large forks during the last three ontogenic stages favours the presence of both
255 microsoils (Hertel 2011) and dendrotelms (Gossner 2018).

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

266

267 Figure 1

268

269 **The effect of management is complex and difficult to assess**

270 Forest management manipulates several factors that may influence the occurrence of TreMs: tree
271 species composition (Vuidot et al. 2011; Larrieu and Cabanettes 2012; Regnery et al. 2013b), tree
272 density (Larrieu et al. 2012, 2014b; Winter et al. 2015), harvesting diameter threshold, the range of
273 tree trunk diameters (Larrieu and Cabanettes 2012), the proportion of remaining habitat-trees after
274 each cutting operation (Winter and Möller 2008; Lassauce et al. 2013) and the density of snags
275 (Vuidot et al. 2011; Larrieu and Cabanettes 2012; Asbeck et al. 2020). Furthermore, harvesting
276 impacts both the density and diversity of TreMs borne by the habitat-trees (Winter and Möller 2008;
277 Larrieu and Cabanettes 2012, Paillet et al. 2017; but see Vuidot et al. 2011 and Winter et al. 2015).

278 Silvicultural practices that favour the removal of trees with undesirable characteristics likely reduce

279 the density of potential habitat-trees, especially during tending operations in young stands and
280 during thinning through the selective removal of “defect-bearing” trees (Martin and Raymond 2019).
281 On the other hand, harvesting of trees can create felling and skidding injuries in the remaining trees,
282 or sun-scalds on smooth-bark species (e.g. beech, cherry). Integrated forest management and other
283 retention forestry approaches may selectively spare, protect and promote habitat-trees (Krumm et
284 al. 2020; Kraus and Krumm 2013).

285 The most relevant factor with regard to management is likely silvicultural practice, especially in the
286 case of systems using clear-cuts, i.e. coppice and coppice with standards, and can be deduced from
287 field observations. To better assess management intensity, it would be useful to consider additional
288 information such as type, frequency and intensity of harvesting operations in selective thinning,
289 target diameter in uneven-aged stands, rotation lengths in even-aged stands, application of TreM
290 retention strategies (and target density of habitat-trees) or the use of tending operations in young
291 stands. Also, the harvesting methods and machinery that are used can have a strong impact on tree
292 injuries and subsequent TreM formation. Horse driven tree removal, for example, will have lower
293 impacts on future TreM development as compared to mechanized techniques, but this former
294 method remains rare and limited to sensitive situations (e.g. bogs) since the productivity of horse-
295 driven logging is low. Such additional information can be obtained from forest managers or by
296 consulting management plans and harvesting records.

297 Management intensity can also be evaluated using indices such as the Forest Management Intensity
298 Index (ForMI, Kahl and Bauhus 2014) or the Silvicultural Management Intensity Indicator (SMI, Schall
299 and Ammer 2013). These indices require additional information that can be challenging to assess
300 post harvesting if you are not the local forest manager (e.g. the proportion of harvested tree volume
301 for ForMI), or require reference data that are not always available (e.g. carrying capacity of a site in
302 terms of basal area for SMI). Time since last harvest has been successfully used as a rough proxy for
303 management intensity (Winter et al. 2015, Regnery et al. 2013b, Paillet et al. 2017), but does not
304 account for a number of management practices that generate specific stand features after decades

305 of set aside. Furthermore, it is important to keep in mind that the dynamics of TreM stock recovery
306 are probably not linear over time (Larrieu et al. 2016; Paillet et al. 2019). Hence, time since last
307 harvest should be modeled using time thresholds that are ecologically significant for determining key
308 changes in TreM occurrence. The inaccuracy of time since the last harvest as a metric, lack of
309 knowledge on the intensity of the last harvest, and our currently poor knowledge of the relevant
310 thresholds for most forest types may explain why this factor had very low explanatory power for
311 predicting TreM occurrence at the tree level in our dataset (Table 1). However, time since harvest
312 does appear to have significant predictive power at the plot and stand scales (Paillet et al. 2017).

313

314 **Trade-off between recording cost of additional features and their relevance for explaining the** 315 **occurrence of TreMs**

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

320

321 Table 3

322

323 **Prioritization of additional site/stand/tree features that could be included in TreM databases**

324 *Acquisition of additional data from databases or in the field*

325 Slope, exposure and altitude can be easily extracted from digital elevation models. However,
326 recording these measurements in the field does not take much time. Presence of cliffs can be
327 evaluated from GIS. However, in the light of preliminary investigations performed in well-studied
328 areas, we argue that it would be more useful to take field measures. Bark feature, phyllotaxis and
329 compartmentalization capacity data need to be gathered from several sources which are available in

330 the literature, and this needs to be done only once, at the tree-species level. However,
331 compartmentalization capacity is currently available for only a few temperate tree species. To
332 compensate for the lack of data at the tree species level, we assume that using data from a given
333 species at the genus level could be an efficient and pertinent first step, while awaiting a more
334 comprehensive assessment (see Larrieu et al. 2021).

335

336 *Additional data that should be recorded in the field*

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

347

348 **Expected value of this additional sampling effort and perspectives**

349 This additional effort in terms of data acquisition could help promote the integration of TreM-related
350 research into the applied field of biodiversity conservation. This would be particularly relevant for
351 models of forest dynamics that include TreM occurrence in order to assess the mid- and long-term
352 effectiveness of forest management strategies for TreM conservation. Work in this direction is

353 ongoing, using for example the spatially explicit, individual-based forest dynamics model Samsara2
354 (Courbaud et al. 2015).

355 TreM conservation will continue to progress if forest managers perform routine assessments of
356 TreMs in the field. To attain this goal, researchers have to identify the most relevant key factors to
357 monitor, while taking into account the extra effort required to add novel measurement protocols to
358 current forest inventory practices. The effectiveness of management regimes in terms of TreM
359 conservation will strongly depend on the motivation of the managers. This requires raising
360 awareness and on-site training, combined with clear and applicable instructions, as well as a
361 justifiable effort when selecting habitat trees. Most managers will be motivated to support such
362 assessments if the above aspects are covered; other avenues may be to offer financial incentives, or
363 by such data collection becoming a part of forest management planning.

364

365 **Conclusion**

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

375

376 **Acknowledgements**

377 We thank Mark Hewison both for his valuable comments and for reviewing the English. We also
378 thank Sylvie Ladet for her expertise on the possibilities to evaluate certain features from GIS and her
379 contribution to the metadata of the international TreM database. M. Svoboda and D. Kozák were
380 supported by the project of the Czech Science Foundation (21-27454S).

381

382 **Bibliography**

383 Asbeck T, Basile M, Stitt J, Bauhus J, Storch I, Vierling KT 2020. Tree-related microhabitats are similar
384 in mountain forests of Europe and North America and their occurrence may be explained by tree
385 functional groups. *Trees* 34: 1453–1466

386 Asbeck T, Grossmann J, Paillet Y, Winiger N, Bauhus J 2021. The Use of Tree-Related Microhabitats as
387 Forest Biodiversity Indicators and to Guide Integrated Forest Management. *Current Forestry Reports*
388 7 (1): 59-68

389 Asbeck T, Pyttel P, Frey J, Bauhus J 2019. Predicting abundance and diversity of tree-related
390 microhabitats in Central European montane forests from common forest attributes. *Forest Ecology*
391 *and Management* 432: 400–408

392 Barthélémy D, Caraglio Y 2007. Plant Architecture: A Dynamic, Multilevel and Comprehensive
393 Approach to Plant Form, Structure and Ontogeny. *Annals of Botany* 99: 375-407

394 Basile M, Asbeck T, Jonker M, Knuff AK, Bauhus J, Braunisch V, Mikusinski G, Storch I 2020. What do
395 tree-related microhabitats tell us about the abundance of forest-dwelling bats, birds, and insects?
396 *Journal Of Environmental Management* 264, # 110401; DOI: 10.1016/j.jenvman.2020.110401

397 Bobiec A, Gutowski JM, Audenslayer WF 2005. The afterlife of the tree. WWF Poland, Warszawa

398 Bouget C, Larrieu L, Nusillard B, Parmain G 2013. In search of the best local habitat drivers for
399 saproxylic beetle diversity in temperate deciduous forests. *Biodivers. Conserv.* 22: 2111–2130

400 Bouget C, Larrieu L, Brin A 2014. Key features for saproxylic beetle diversity derived from rapid
401 habitat assessment in temperate forests. *Ecol. Indic.* 36: 656–664

402 Bouget C., Parmain G., Gilg O., Noblecourt T., Nusillard B., Paillet Y., Pernot C., Larrieu L., Gosselin F.
403 2014. Does a set aside conservation strategy help restore old-growth attributes and conserve
404 saproxylic beetles in temperate forests? *Animal Conservation*, 17: 342–353.

405 Breda N, Granier A, Aussenac G 2004. La sécheresse de 2003 dans le contexte des 54 dernières
406 années: analyse écophysiological et influence sur les arbres forestiers. *Revue Forestière Française*,
407 vol. LVI (2): 109-131

408 Bryan JA, Lanner RM 1981. Epicormic branching in rocky mountain douglas-fir. *Canadian Journal of*
409 *Forest Research* 11: 190–200

410 Bürkner P 2021. Bayesian Item Response Modeling in R with brms and Stan. *Journal of Statistical*
411 *Software* 100(5): 1–54

412 Bütler R, Lachat T, Larrieu L, Paillet Y 2013. Habitat trees: key elements for forest biodiversity. Kraus
413 D., Krumm F. (Eds.), Integrative Approaches as an Opportunity For the Conservation of Forest
414 Biodiversity. European Forest Institute, Freiburg, DEU, p84–91

415 Chomicki G, Coiro M, Renner SS 2017. Evolution and ecology of plant architecture: integrating
416 insights from the fossil record, extant morphology, developmental genetics and phylogenies. *Annals
417 of Botany* 120: 855-891

418 Courbaud B, Lafond V, Lagarrigues G, Vieilledent G, Cordonnier T, Jabot F, De Coligny F 2015.
419 Applying ecological model evaluation: lessons learned with the forest dynamics model Samsara2.
420 *Ecological Modelling* 314: 1–14

421 Courbaud B, Larrieu L, Kozak D, Kraus D, Lachat T, Ladet S, Müller J, Paillet Y, Sagheb-Talebi K, Schuck
422 A, Stillhard J, Svoboda M, Zudin S 2021. Factors influencing the rate of formation of tree-related
423 microhabitats and implications for biodiversity conservation and forest management. *J Appl Ecol.* 00:
424 1–12

425 Courbaud B, Pupin C, Letort A, Cabanettes A, Larrieu L 2017. Modelling the probability of
426 microhabitat formation on trees using cross-sectional data. *Methods in Ecology and Evolution* 8:
427 1347-1359

428 Crook MJ, Ennos AR, Banks JR 1997. The function of buttress roots: a comparative study of the
429 anchorage systems of buttressed (*Aglaia* and *Nephelium ramboutan* species) and non-buttressed
430 (*Mallotus wrayi*) tropical trees. *Journal of Experimental Botany*, Vol 48, n° 314: 1703-1716

431 Daina P, Drénou C 2021. Lettura e previsione. Il metodo ARCHI per valutare lo stato fisiologico dei
432 Pini. *Acer.* 2: 40-46

433 Dorren LKA, Berger F 2006. Stem breakage of trees and energy dissipation during rockfall impacts.
434 *Tree Physiology* 26: 63-71

435 Drénou C, 2017. L’arbre au-delà des idées reçues. CNPF; Paris

436 Drénou C 1994. Approche architecturale de la sénescence des arbres, le cas de quelques
437 angiospermes tempérées et tropicales. Thèse de doctorat, Univ. de Montpellier II, 263 p.

438 Drénou C 2000. Pruning trees: the problem of forks; *Journal of Arboriculture* 26(5): 264-269

439 Drénou C, Bouvier M, Lemaire J 2015. The diagnostic method ARCHI applied on declining
440 pedunculate oaks. *Arboricultural Journal* 37(3) : 166-179

441 Drénou C, Caraglio Y 2019. Parlez-vous ARCHI? Les principales définitions de la méthode ARCHI. *Forêt
442 Entreprise* 246 : 28-35

443 Drénou C, Piazzetta R, Lecomte B, Mariton B 2019. La méthode Archi appliquée au chêne-liège
444 (*Quercus suber* L.). *Forêt méditerranéenne* XL (1): 55-66

445 Drénou C, Restrepo D, Slater D 2020. Demystifying Tree Forks: Vices and Virtues of Forks in
446 *Arboriculture. J. Bot. Res.* 3(1): 100-113

447 Dujesiefken D, Drénou C, Oven P, Stobbe H 2005. Arboricultural practices. pp. 419-441. Konijnendijk
448 C., Nilsson K., Randrup T.B., Schipperijn J. Eds. « Urban Forests and Trees », Springer, 520 p.

449 Dujesiefken D, Liese W 2011. The CODIT principle. New results about wound reactions of trees.
450 *Arborist News*, 20(2): 28-30.

451 Dujesiefken D, Liese W 2015. The CODIT Principle: Implications for Best Practices. USA: International
452 Society of Arboriculture.

453 Dujesiefken D, Fay N, de Groot JW, de Berker N 2016. Trees, a Lifespan Approach - Contributions to
454 arboriculture from European practitioners. Foundation for Sustainable Development and Roads for
455 Nature, 133 p.

456 Dumé G, Gauberville C, Mansion D, Rameau JC, Bardat J, Bruno E, Keller R. 2018. Flore Forestière
457 Française, guide écologique illustré. Tome 1 Plaines et collines; Nouvelle édition; CNPF, Paris

458 Ennos AR 1993. The function and formation of buttresses. Trends in Ecology & Evolution 8: 350-351

459 Everhart SE, Ely JS, Keller HW 2009. Evaluation of tree canopy epiphytes and bark characteristics
460 associated with the presence of corticolous myxomycetes. Botany 87: 509-517

461 Finn JA 2001. Ephemeral resource patches as model systems for diversity-function experiments.
462 Oikos 92 : 363–366

463 Fournier M, Bonnesoeur V, Deleuze C, Renaud JP, Legay M, Constant T, Moulia B 2015. Pas de vent,
464 pas de bois. L'apport de la biomécanique des arbres pour comprendre la croissance puis la
465 vulnérabilité aux vents forts des peuplements forestiers. RFF 3: 213-237

466 Fritz O, Brunet J, Caldiz M 2009. Interacting effects of tree characteristics on the occurrence of rare
467 epiphytes in a Swedish beech forest area. Bryologist 112: 488-505

468 Gardiner B, Peltola H, Kellomäki S 2000. Comparison of two models for predicting the critical wind
469 speeds required to damage coniferous trees. Ecol. Model. 129: 1– 23

470 Gilman EF 2011. An illustrative guide to pruning – Third edition. Delmar Publishers.

471 Gleißner P 1998. Das Verzweigungsmuster ausgewählter Laubbaumarten und seine Veränderung
472 durch nicht-pathogene Schädigungen. Palmarum Hortus Francofurtensis 6: 3–132

473 Gosselin F, Larrieu L 2020. Developing and using statistical tools to estimate observer effect for
474 ordered class data: The case of the IBP (Index of Biodiversity Potential). Ecological Indicators 110:
475 105884

476 Gossner MM 2018. A three year study of the phenology of insect larvae (Coleoptera, Diptera) in
477 water-filled tree holes in the canopy of a beech tree. European Journal of Entomology 115: 524-534

478 Hadfield JD 2010. MCMC Methods for Multi-Response Generalized Linear Mixed Models: The
479 MCMCglmm R Package. Journal of Statistical Software 33(2): 1-22. URL
480 <https://www.jstatsoft.org/v33/i02/>.

481 Halama M, Chachula P, Rutkowski R 2014. *Mycena Juniperina* (Agaricales, Basidiomycota), new for
482 the Polish and central European mycobiota. Polish Botanical Journal 59(1): 109–116

483 Hallé F., Oldeman R. 1970. Essai sur l'architecture et la dynamique de croissance des arbres
484 tropicaux. Paris, Masson, 192 p

485 Herrault PA, Larrieu L, Cordier S, Gimmi U, Lachat T, Ouin A, Sarthou JP, Sheeren D 2016. Combined
486 effects of area, connectivity, history and structural heterogeneity of woodlands on the species
487 richness of hoverflies (Diptera: Syrphidae). Landsc. Ecol. 31: 877–893

488 Hertel D 2011. Tree roots in canopy soils of old European beech trees. An ecological reassessment of
489 a forgotten phenomenon. Pedobiologia 54: 119-125

- 490 Heuret P, Barthélémy D, Guédon Y, Coulmier X, Tancre J 2002. Synchronisation of growth, branching
491 and flowering processes on an individual and stand level in the South American tropical tree *Cecropia*
492 *obtuse* Trécul (Cecropiaceae). *American Journal of Botany* 89(7): 1180-1187
- 493 Hirons AD, Thomas PA 2018. *Applied tree biology*. Wiley Blackwell, 432 p
- 494 Jahed RR, Kavousi MR, Farashiani ME, Talebi KS, Babanezh M, Courbaud B, Wirtz R, Müller J, Larrieu
495 L 2020. A Comparison of the Formation Rates and Composition of Tree-Related Microhabitats in
496 Beech Dominated Primeval Carpathian and Hyrcanian Forests. *Forests* 11, 144; doi:
497 10.3390/f11020144
- 498 Joye T 2019. Tree architecture, a valuable (old) new tool. *The Arboricultural Association*. ARB
499 magazine 185: 44-48
- 500 Kahl T, Bauhus J 2014. An index of forest management intensity based on assessment of harvested
501 tree volume, tree species composition and dead wood origin. *Nature Conservation* 7: 15–27. doi:
502 10.3897/natureconservation.7.7281
- 503 Komonen A, Müller J 2018. Dispersal ecology of deadwood organisms and connectivity conservation.
504 *Conservation Biology* 32: 535-545
- 505 Kozák D, Mikoláš M, Svitok M, Bače R, Paillet Y, Larrieu L, Nagel TA, Begovič K, Čada V, Diku A,
506 Frankovič M, Janda P, Kameniar O, Keren S, Kjučukov P, Lábusová J, Langbehn T, Málek J, Mikac S,
507 Morrissey RC, Nováková M, Schurrman JS, Svobodová K, Synek M, Teodosiu M, Toromani E, Trotsiuk
508 V, Vítková L, Svoboda M 2018. Profile of tree-related microhabitats in European primary beech-
509 dominated forests. *Forest Ecology and Management* 429: 363–374
- 510 Kraus D, Krumm F (eds) 2013. *Integrative approaches as an opportunity for the conservation of forest*
511 *biodiversity*. European Forest Institute.
- 512 Kraus D, Schuck A, Bebi P, Blaschke M, Bütler R, Flade M, Heintz W, Krumm F, Lachat T, Larrieu L,
513 Lehnerova L, Levin M, Mergner U, Pach M, Paillet Y, Pyttel P, Rydkvist T, Santopuoli G, Sever K, Sturm
514 K, Vandekerkhove K, Winter S, Witz M, Winnock M, Marcandella M, Roth I, Jakob A, Dickele R,
515 Hofmann G, Ruis-Eckhardt D, Boschen S, Schölmerich U, Leder B, Guericke M, Merkel H, Löffler D,
516 Schusser S, Runkel M, Steinmetz A, Marx KH, Mongelluzzi A, Wilshusen F, Boutteaux J, Duchamp L,
517 Dericbourg N, Rouyer E, Csikos V, Sweeny K, Steichen D, Leytem M, Konczal S, Stereńczak K,
518 Kazimirovic M, Šebeň V, Baiges Zapater T, van der Maaten-Theunissen M, Pommer A, Nord-Larsen T,
519 Fuhr M, Delebeque L, Navarro LM, Lasala D, Waez-Mousavi S, Sefidi K, Abellanas B, Zudin S 2021.
520 Spatially explicit database of tree related microhabitats (TreMs). Version 1.15. Institut national de
521 recherche pour l'agriculture, l'alimentation et l'environnement (INRAE).
- 522 de Kroon H, Huber H, Stuefer JF, van Groenendael JM 2005. A modular concept of phenotypic
523 plasticity in plants. *New Phytologist* 166: 73–82
- 524 Krumm F, Schuck A, Rigling A (eds) 2020. *How to balance forestry and biodiversity conservation – A*
525 *view across Europe*. European Forest Institute (EFI); Swiss Federal Institute for Forest, Snow and
526 *Landscape Research (WSL)*, Birmensdorf
- 527 Lachaud S, Bonnemain JL 1981. Xylogénèse chez les Dicotylédones arborescentes. I. Modalités de la
528 remise en activité du cambium et de la xylogénèse chez les hêtres et les chênes âgés. *Can. J. Bot.* 59
529 (7): 1222-1230

530 Lambert J, Drénou C, Denux JP, Balent G, Chéret V 2013. Monitoring forest decline through remote
531 sensing time series analysis. *GIScience & Remote Sensing* 50 (4) : 437-457

532 Larrieu 2014. Les dendromicrohabitats; facteurs clés de leur occurrence dans les peuplements
533 forestiers, impact de la gestion et relations avec la biodiversité taxonomique. PhD thesis. University
534 of Toulouse

535 Larrieu L, Bouget C 2017. Could TReMs be relevant conservation forestry targets and/or biodiversity
536 indicators? In: European workshop : Monitoring of saproxylic beetles and other insects protected in
537 the European Union, 24-26/05/2017, Mantova, Italy. [https://oatao.univ-](https://oatao.univ-toulouse.fr/21930/1/Larrieu_21930.pdf)
538 [toulouse.fr/21930/1/Larrieu_21930.pdf](https://oatao.univ-toulouse.fr/21930/1/Larrieu_21930.pdf)

539 Larrieu L, Cabanettes A 2012. Species, live status, and diameter are important tree features for
540 diversity and abundance of tree microhabitats in subnatural montane beech-fir forests. *Can. J. For.*
541 *Res.* 42: 1433–1445

542 Larrieu L, Cabanettes A, Brin A, Bouget C, Deconchat M 2014b. Tree microhabitats at the stand scale
543 in montane beech-fir forests: practical information for taxa conservation in forestry. *Eur. J. For. Res.*
544 133: 355–367

545 Larrieu L, Cabanettes A, Courbaud B, Goulard M, Heintz W, Kozak D, Kraus D, Lachat T, Ladet S,
546 Müller J, Paillet Y, Schuck A, Stillhard J, Svoboda M 2021. Co-occurrence patterns of tree-related
547 microhabitats: A method to simplify routine monitoring. *Ecological Indicators* 127: 107757

548 Larrieu L, Cabanettes A, Delarue A 2012. Impact of silviculture on dead wood and on the distribution
549 and frequency of tree microhabitats in montane beech-fir forests of the Pyrenees. *Eur. J. For. Res.*
550 131: 773–786

551 Larrieu L, Cabanettes A, Gonin P, Lachat T, Paillet Y, Winter S, Bouget C, Deconchat M 2014c.
552 Deadwood and tree microhabitat dynamics in unharvested temperate mountain mixed forests: a life-
553 cycle approach to biodiversity monitoring. *For. Ecol. Manag.* 334: 163–173

554 Larrieu L, Cabanettes A, Goux N, Burnel L, Bouget C, Deconchat M 2016. Development over time of
555 the tree-related microhabitat profile: the case of lowland beech–oak coppice-with-standards set-
556 aside stands in France. *Eur. J. For. Res.* 136: 37–49. DOI 10.1007/s10342-016-1006-3

557 Larrieu L, Gonin P 2008. L'indice de Biodiversité Potentielle (IBP) : une méthode simple et rapide pour
558 évaluer la biodiversité potentielle des peuplements forestiers. *Rev. For. Fr.* 06: 727-748

559 Larrieu L, Gosselin F, Archaux F, Chevalier R, Corriol G, Dauffy-Richard E, Deconchat M, Gosselin M,
560 Ladet S, Savoie JM, Tillon L, Bouget C 2019. Assessing the potential of routine structural and
561 dendrometric variables as potential habitat surrogates from multi-taxon data in European temperate
562 forests. *Ecological Indicators* 104: 116–126

563 Larrieu L, Paillet Y, Winter S, Bütler R, Kraus D, Krumm F, Lachat T, Michel AK, Regnery B,
564 Vandekerckhove K 2018. Tree related microhabitats in temperate and Mediterranean European
565 forests: A hierarchical typology for inventory standardization. *Ecological Indicators* 84: 194-207
566 Larson D.W., Matthes-Sears U., Kelly P.E. 1993. Cambial dieback and partial shoot mortality in cliff-face
567 *Thuja occidentalis*: evidence for sectorized radial architecture. *Int. J. Plant Sci.* 154(4): 496-505

568 Lassauce A, Larrieu L, Paillet Y, Lieutier F, Bouget C 2013. The effects of forest age on saproxylic
569 beetle biodiversity: implications of shortened and extended rotation lengths in a French oak high
570 forest. *Insect Conservation and Diversity* 6: 396-410

571 Lebourgeois F, Drénou C, Bouvier M, Lemaire J 2015. Caractérisation de la croissance des chênaies
572 pédonculées atlantiques dépérissantes : effets des sécheresses et relation avec l'architecture des
573 houppiers. Rev. For. Fr. LXVII (4): 333-351

574 López, R. E., Holle R. L., Heitkamp T. A. 1995. Lightning Casualties and Property Damage in Colorado
575 from 1950 to 1991 Based on Storm Data. Weather and Forecasting 10:114-126.

576 Martin M, Raymond P 2019. Assessing tree-related microhabitat retention according to a harvest
577 gradient using tree-defect surveys as proxies in Eastern Canadian mixedwood forests. The Forestry
578 Chronicle 95(3): 157-170

579 Mattheck C., 1991. Trees, the mechanical design. Springer Verlag, 121 p.

580 McElreath R 2020. Statistical Rethinking. A Bayesian Course with Examples in R and STAN. Second
581 Edition. Chapman & Hall, Texts in Statistical Science. 593p.

582 Michel AK, Winter S 2009. Tree microhabitat structures as indicators of biodiversity in Douglas-fir
583 forests of different stand ages and management histories in the Pacific Northwest, U.S.A. For. Ecol.
584 Manag. 257: 1453–1464

585 Moss EH, Gorham AL 1953. Interxylary cork and fission of stems and roots. Phytomorphology 3: 285-
586 294

587 Nicolini E, Barthélémy D, Heuret P 2000. Influence de la densité du couvert forestier sur le
588 développement architectural de jeunes chênes sessiles, *Quercus petraea* (Matt.) Liebl. (*Fagaceae*), en
589 régénération forestière. Canadian Journal of Botany 78: 1531-1544

590 Nicolini E, Caraglio Y 1994. L'influence de divers caractères architecturaux sur l'apparition de la
591 fourche chez le *Fagus sylvatica*, en fonction de l'absence ou de la présence d'un couvert. Canadian
592 Journal of Botany 72 (12): 1723-1734

593 Nicolini E, Caraglio Y, Pelissier R, Leroy C, Roggy JC 2003. Epicormic branches, a growth indicator for a
594 tropical forest tree, *Dicorynia guianensis* Amshoff (Caesalpiaceae). Annals of Botany 92(1): 97-105

595 Nordén B, Dahlberg A, Brandrud TE, Fritz O, Ejrnaes R, Ovaskainen O 2014. Effects of ecological
596 continuity on species richness and composition in forests and woodlands: A review. Ecoscience 21:
597 34-45

598 Norton DA, Carpenter MA 1998. Mistletoes as parasites: host specificity and speciation. Trends Ecol.
599 Evol. 13: 101–05

600 Oliva J, Colinas C 2010. Epidemiology of *Heterobasidion abietinum* and *Viscum album* on silver fir
601 (*Abies alba*) stands of the Pyrenees. For. Path. 40: 19–32. doi: 10.1111/j.1439-0329.2009.00603.x

602 Oven P, Torelli N 1999. Response of the cambial zone in conifers to wounding. Phytomorphology (Horn, Austria)
603 39(3): 133-137.

604 Paillet Y, Archaux F, du Puy S, Bouget C, Boulanger V, Debaive N, Gilg O, Gosselin F, Guilbert E 2018.
605 The indicator side of tree microhabitats: A multi-taxon approach based on bats, birds and saproxylic
606 beetles. Journal of Applied Ecology 55(5): 2147-2159

607 Paillet Y, Archaux F, Boulanger V, Debaive N, Fuhr M, Gilg O, Gosselin F, Guilbert E 2017. Snags and
608 large trees drive higher tree microhabitat densities in strict forest reserves. For. Ecol. Manag. 389:
609 176–186

610 Paillet Y, Debaive N, Archaux F, Cateau E, Gilg O, Guilbert E 2019. Nothing else matters? Tree
611 diameter and living status have more effects than biogeoclimatic context on microhabitat number
612 and occurrence: An analysis in French forest reserves. PLoS ONE 14(5): e0216500.
613 <https://doi.org/10.1371/journal.pone.0216500>

614 Paillet, Y., C. Pernot, V. Boulanger, N. Debaive, M. Fuhr, O. Gilg, and F. Gosselin. 2015. Quantifying
615 the recovery of old-growth attributes in forest reserves: A first reference for France. *Forest Ecology
616 and Management* 346:51-64.

617 Pavlin J, Nagel TA, Svitok M, Pettit JL, Begović K, Mikac S, Dikku A, Toromani E, Panayotov M,
618 Zlatanov T, Haruta O, Dorog S, Chaskovskyy O, Mikoláš M, Janda P, Frankovič M, Rodrigo R, Vostarek
619 O, Synek M, Dušátko M, Kníř T, Kozák D, Kameniar O, Bače R, Čada V, Trotsiuk V, Schurman JS,
620 Saulnier M, Buechling A, Svoboda M 2021. Disturbance history is a key driver of tree life span in
621 temperate primary forests. *Journal of Vegetation Science* 32: e13069

622 Pearcy RW, Muraoka H, Valladares F 2005. Crown architecture in sun and shade environments:
623 assessing function and tradeoffs with a 3-D simulation model. *New Phytologist* 166: 791–800

624 Perré P, Badel E 2006. De l'eau dans l'arbre à l'eau dans le matériau bois – Une introduction. *Revue
625 Forestière Française LVIII (4): 305-315*

626 Petty JA, Swain C 1985. Factors influencing stem breakage in conifers in high winds. *Forestry* 58: 75 –
627 84

628 Pettit JL, Pettit JM, Janda P, Rydval M, Čada V, Schurman JS, Nagel TA, Bače R, Saulnier M, Hofmeister
629 J, Matula R, Kozák D, Frankovič M, Turcu DO, Mikoláš M, Svoboda M.2021. Both Cyclone-induced and
630 Convective Storms Drive Disturbance Patterns in European Primary Beech Forests. *Journal of
631 Geophysical Research: Atmospheres* 126: e2020JD033929

632 Puverel C, Abourachid A, Bohmer C, Leban JM, Svoboda M, Paillet Y 2019. This is my spot: What are
633 the characteristics of the trees excavated by the Black Woodpecker? A case study in two managed
634 French forests. *Forest Ecology and Management* 453: 117621

635 Rameau JC, Mansion D, Dumé G 1991. *Flore Forestière Française, Tome 1: Plaines et Collines*. Institut
636 pour le Développement Forestier. Paris

637 Regnery B, Couvet D, Kubarek L, Julien JF, Kerbiriou C 2013a. Tree microhabitats as indicators of bird
638 and bat communities in Mediterranean forests. *Ecol. Indic.* 34: 221–230

639 Regnery B, Paillet Y, Couvet D, Kerbiriou C 2013b. Which factors influence the occurrence and density
640 of tree microhabitats in Mediterranean oak forests? *For. Ecol. Manag.* 295: 118–125

641 Roloff A 1988. Morphologie der Kronenentwicklung von *Fagus sylvatica* L. (Rotbuche) unter
642 besonderer Berücksichtigung neuartiger Veränderungen. II. Strategie der Luftraumeroberung und
643 Veränderung durch Umwelteinflüsse. *Flora* 180: 297–338

644 Rutishauer E, Barthélémy D, Blanc L, Nicolini EA 2011. Crown fragmentation assessment in tropical
645 trees: Method, insights and perspectives. *Forest Ecology and Management* 261 : 400-407

646 Sabatier S, Barthélémy D 1995. Architecture du cèdre de l'Atlas, *Cedrus atlantica* (Endl.) Manetti ex
647 Carrière (Pinaceae). Bouchon Jean (ed.). *Architecture des arbres fruitiers et forestiers*. INRA. Paris :
648 157-173. ISBN 2-7380-0623-X

649 Sabatier S, Caraglio Y, Drénou C 2014. L'architecture des arbres aux services des forestiers.
650 Innovations Agronomiques 41: 119-128

651 Schall P, Ammer C 2013. How to quantify forest management intensity in Central European forests.
652 European Journal of Forest Research 132(2): 379–396. doi: 10.1007/s10342-013- 0681-6

653 Schneuwly-Bollschweiler M, Schneuwly DM 2012. How fast do European conifers overgrow wounds
654 inflicted by rockfall? Tree Physiology 00: 1–8

655 Slater D 2018. The association between natural braces and the development of bark-included
656 junctions in trees. Arboricultural Journal 40(1): 16-38

657 Smith KT 2015. Compartmentalization, Resource Allocation, and Wood Quality. Current Forestry
658 Reports 1: 8-15

659 Stobbe H, Kleist G, Dujesiefken D 1998. Die Hamburger Schnittmethode. Grundlagen und neue
660 Erkenntnisse. Jahrbuch der Baumpflege, Bernhard Thalacker Verlag, Braunschweig, p. 184-193.

661 Stokland JN, Siitonen J, Jonsson BG 2012. Biodiversity in Dead Wood. Cambridge

662 Stokes A, Salin F, Kokutse AD, Berthier S, Jeannin H, Mochan S, Dorren L, Kokutse N, Abd Ghani M,
663 Fourcaud T 2005. Mechanical resistance of different tree species to rockfall in the French Alps. Plant
664 and Soil 278: 107-117

665 Trabucco A, Zomer RJ 2010. Global Soil Water Balance Geospatial Database. CGIAR Consortium for
666 Spatial Information. Published online, available from the CGIAR-CSI GeoPortal. Retrieved from
667 <http://www.cgiar-csi.org>.

668 Trouy MC 2015. Anatomie du bois, formations, fonctions et identification. Quae édit.; 151 p.

669 Verheyden H, Ballon P, Bernard V, Saint-Andrieux C 2006. Variations in bark-stripping by red deer
670 *Cervus elaphus* across Europe. Mammal Review 36: 217-234

671 Vesk PA 2006. Plant size and resprouting ability: trading tolerance and avoidance of damage? Ecology
672 94: 1027–1034

673 Villarreal M, Esteve-Raventos . 1999. *Mycena conicoalba*, a new corticolous species from Spain.
674 Österr.Z. Pilzk. 8 : 15-34

675 Vuidot A, Paillet Y, Archaux F, Gosselin F 2011. Influence of tree characteristics and forest
676 management on tree microhabitats. Biol. Conserv. 144: 441–450

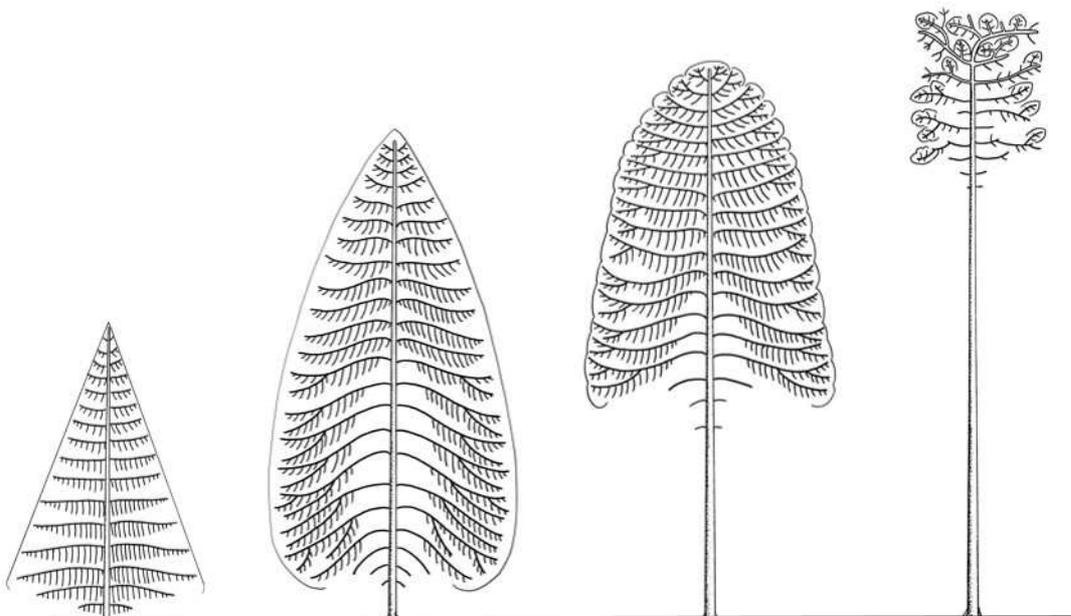
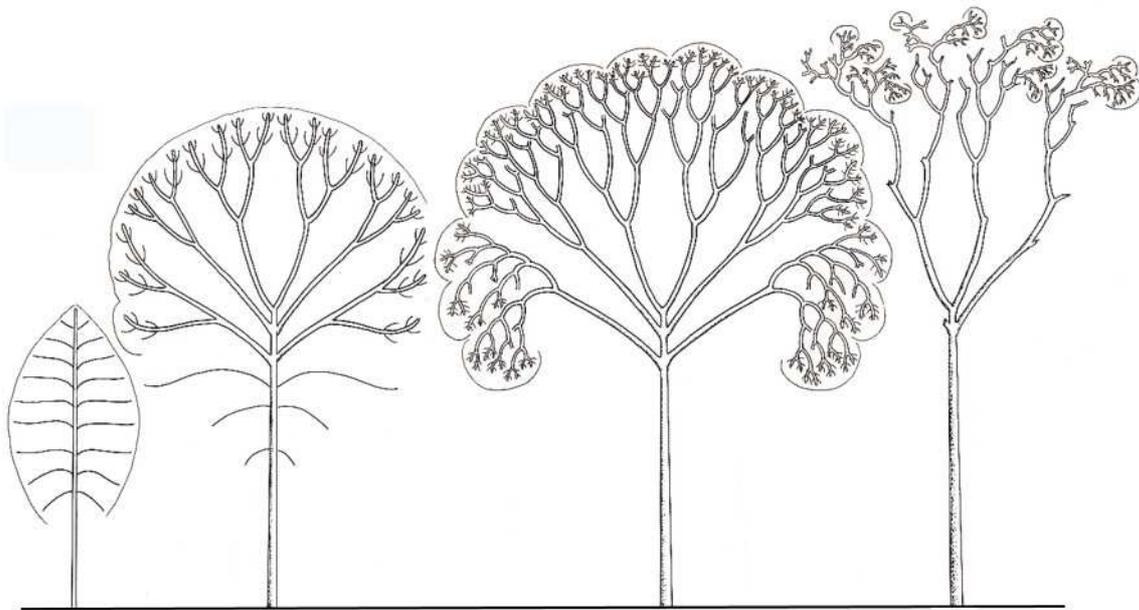
677 Walker W, Baccini A, Nepstad M, Horning N, Knight D, Braun E, Bausch A 2011. Field Guide for Forest
678 Biomass and Carbon Estimation. Version 1.0.

679 Winter S, Möller GC 2008. Microhabitats in lowland beech forests as monitoring tool for nature
680 conservation. For. Ecol. Manag. 255: 1251–1261

681 Winter S, Höfler J, Michel AK, Böck A, Ankerst DP 2015. Association of tree and plot characteristics
682 with microhabitat formation in European beech and Douglas-fir forests. Eur. J. For. Res. 134: 335–347

683

Figure captions



2

3

4 **Figure 1. Ontogenic dynamics of tree growth**

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

13

Table 1. Proportion of variance explained by the full and simplified models for predicting the occurrence of tree-related microhabitats (TreM).

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

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

*resulted from an exceptional bad fit that could not be improved

Table 2. Potential key factors for TreM formation

Effect on TreM formation: *** 'highly probable', * 'probable'

Scale and Type of factors	Factor	Potential relationship with TreMs	References	TreM group (with types belonging to the group that are likely to be particularly impacted)
Site; Environmental conditions	Unfavourable conditions for tree growth	Direct sun exposure, poor soil and low precipitation, faster ontogenic dynamics	Barthélémy and Caraglio (2007); Nicolini and Caraglio (1994); de Kroon et al. (2005); Pearcy et al. (2005) ; Sabatier and Barthélémy (1995)	*Crown deadwood *Rot holes *Exposed sapwood and heartwood (Cracks)
	South-facing slope	Increases abundance of Mistletoe	Oliva and Colinas (2010)	*Epiphytic and parasitic crypto- and phanerogams (Mistletoe)
	Altitude	Humid climate favours epiphytic plants	Rameau et al. (1991)	***Epiphytic and parasitic crypto- and phanerogams (Lichen, Liana, Mosses)
	Fertile soil	Favours epiphytic plants	Rameau et al. (1991)	***Epiphytic and parasitic crypto- and phanerogams (Lichen, Liana, Mosses)
		Favours tree species with non-acid barks (e.g. ash, poplars, sycamore)	Rameau et al. (1991)	*Epiphytic and parasitic crypto- and phanerogams (Lichen, Liana, Mosses)
	Thin or compact soils	Favours buttress formation	Ennos (1993)	***Concavities (Buttress root concavities)
		Thin soils favour branch death	Breda et al. (2004)	***Crown deadwood (Dead branches ; dead top)

	Wind	Favours buttress formation (reaction wood)	Crook et al. (1997); Fournier et al. (2015)	***Concavities (Buttress root concavities)
		Strong wind events lead to breakages	Gardiner et al. (2000); Petty and Swain (1985)	***Exposed sapwood and heartwood (Stem breakage; Limb breakage; Fork split at the intersection) ***Crown deadwood (Remaining broken limb)
	Cliffs	Cliffs up slope or mobile scree favour wounds and stem breakage by stone impacts	Dorren and Berger (2006); Stokes et al. 2005	***Exposed sapwood (Bark loss) *** Exposed sapwood and heartwood (Stem breakage)
	Steep slopes	Favours buttress formation (reaction wood)	Fournier et al. (2015)	*Concavities (Buttress root concavities)
	Mountain summits and ridges	Locations prone to lightning strikes	López et al. (1995)	* Exposed sapwood and heartwood (Lighting scars)
Stand; Stand features	High tree density	Favours high trunks without branches	Barthélémy and Caraglio (2007); Nicolini and Caraglio (1994); Nicolini et al. (2000)	*Woodpecker breeding cavities (Large woodpecker breeding cavity)
		Favours development of accidental forks including bark, prone to fork breakage	Slater (2018)	***Exposed sapwood and heartwood (Fork split at the intersection)
	Spatial distribution of trees	Tree clustering is detrimental to	Puverel et al. (2019)	*Woodpecker breeding cavities (Large

		cavity digging by woodpeckers		woodpecker breeding cavity)	
Tree; Tree species	Low compartmentalization capacity	Favours fungi and decay	Dujesiefken and Liese (2011); Smith (2015)	***Rot holes	
	Presence of heartwood	Heartwood absent in young trees, sometimes for a long period (e.g. 25-70 years for <i>Fagus sylvatica</i>), hinders rot-hole dynamics	Trouy (2015)	*Rot holes	
	Phyllotaxis	Greater occurrence of bark embedded in the wood for species with decussate opposite phyllotaxis	Drénou (2000); Stobbe et al. (1998)	Exposed sapwood and heartwood (***Fork split at the intersection;*Crack)	
	Tree architecture (forks):	Some architectural models (e.g. Troll's model; Hallé and Oldemann 1970) produce recurrent forks with weak anchoring throughout their lifetime (e.g. <i>Ulmus</i> spp., <i>Tilia</i> spp.)	Chomicki et al. (2017); Drénou (2000); Heuret et al. (2002)	*Exposed sapwood and heartwood (Fork split at the intersection)	
	Bark features		Rough bark (e.g. <i>Quercus</i> spp., <i>Juniperus</i> spp.) favours formation of bark microsoils	Villarreal and Esteve-Raventos (1999); Halama et al. (2014)	***Microsoils
			High bark pH favours mosses	Fritz et al. (2009)	***Epiphytic and parasitic crypto- and phanerogams (Mosses)

		Smooth and hydrophobe barks are unfavourable to plasmodial slime moulds	Everhart et al. 2009	*Ephemeral fungal fruiting bodies and slime moulds (Myxomycetes)
	Mistletoe	Mistletoe has specific hosts	Norton and Carpenter (1998)	***Epiphytic and parasitic crypto- and phanerogams (Mistletoe)
Tree; age	Tree age	The probability for the tree to be wounded and infected with decay increases with tree age	Dujesiefken et al. (2016); Smith (2015)	***Rot holes
		Young trees have very wet sapwood sensitive to frost	Perré and Badel (2006); Walker et al. (2011)	*Exposed sapwood and heartwood (Cracks)
Tree; ontogenesis	Development stage	Compartmentalization capacity decreases as the development stage takes a step forward	Smith (2015)	***Rot holes
		Development stage is characterized by the establishment of main forks (no accidental forks): young stage = no forks, adult = 1-4 forks, mature = 5-10 forks, senescent >10 forks	Chomicki et al. (2017); Drénou et al. (2000, 2019); Drénou and Caraglio (2019); Gleißner (1998); Roloff (1988)	*Concavities (Dendrotelms) * Exposed sapwood and heartwood (Cracks) *Microsoils
		Irregularization of the cambial activity during ontogenesis	Larson et al. (1993); Lachaud and Bonnemain (1981); Moss and Gorham (1953)	*Concavities

		The senescent stage is characterized by sun-exposed dead branches	Rutishauer et al. (2011); Gleißner (1998); Roloff (1988)	***Crown deadwood
		Limited ability to react at the senescent stage	Drénou (1994); Nicolini et al. (2003); Bryan and Lanner (1981); Vesk (2006)	***Crown deadwood **Exposed sapwood and heartwood *Epiphytic and parasitic crypto- and phanerogams (Lichen, Mistletoe) *Perennial fungal fruiting bodies *Ephemeral fungal fruiting bodies and slime moulds
		The disappearance of the root pivot during senescent stage favours buttress formation	Mattheck (1991)	*Concavities (Buttress root concavities)
Tree; Physiological state	Tree physiological state	Impacts both biomechanics of epicormic shoots (weak anchoring) and dead branch presence	Hirons and Thomas (2018); Lebourgeois et al. (2015); Drénou et al. (2015)	***Crown deadwood *Exposed sapwood and heartwood *Perennial fungal fruiting bodies *Ephemeral fungal fruiting bodies and slime moulds

Table 3. Assessment of the compromise between recording cost of additional features which might be assessed in future studies and their relevance for explaining the occurrence of Tree-related Microhabitat (TreM) groups; cost: time for recording or technology requiring specific skills; relevance: the number of tree-related microhabitats potentially affected and the magnitude of expected effect

Grain	Feature	At the laboratory	In the field	Cost	Relevance for explaining the occurrence of TreM groups	Remarks	Trade-off
Stand/plot	Slope	Digital Elevation Model	Using clinometer	Very low	1 TreM group potentially affected with a low magnitude of expected effect.	Field measurements provide more accurate estimates and incorporate spatial variability.	Fairly good
	Exposure	Digital Elevation Model	Using compass	Very low	1 TreM group potentially affected with a low magnitude of expected effect.	Field measurements provide more accurate estimates and incorporate spatial variability.	Fairly good
	Presence of cliffs	Digital Elevation Model (e.g. selecting slopes over 80°)	Direct observation	Low	2 TreM groups potentially affected; the magnitude of expected effect is very high.	Preliminary investigations in well-studied areas showed this method is not sufficiently sensitive for detecting small cliffs.	Good
	Altitude	Digital Elevation Model	Using altimeter	Very low	1 TreM group potentially affected; the magnitude of expected effect is very high.	Asbeck et al. (2019) showed that increasing altitude favours the number of buttress-root concavities and epiphytic lichens, while mosses and mistletoe are more abundant at lower altitudes.	Good

Soil fertility	Geological data on GIS	For nutrients: Humus forms, flora, pH at the soil surface layer, or tree size (e.g. by the total height at a given age) when the stand is mature For water storage capacity: recording depth, the proportion of coarse fragments and textures for each layer	High (in the field)	5 TreM groups potentially affected and the magnitude of expected effects are rather high for 3 groups.	Geological data only takes nutrient richness into account and ignores soil water storage; it therefore needs to be complemented by additional datasets focusing on soil hydraulic properties or water balance (e.g. Global Soil Water Balance Geospatial Database; see Trabucco and Zomer 2010). Observers need to be well trained to use such methods for qualifying soil features in the field. Measuring soil depth quickly requires specialized tools such as an auger and the presence of coarse fragments (even when not abundant) may cause difficulties for penetrating the soil, leading to an underestimation of soil depth.	Bad
Topographic situations exposed to strong wind or lightning	GIS	Field assessment	Low	3 TreM groups potentially affected by high wind speeds and the magnitude of	Wind speed is very difficult to assess at the stand level even though ridges and passes are more prone to high wind speeds.	Fairly bad

					<p>expected effect is high.</p> <p>1 TreM group potentially affected by lightning strikes with a low magnitude of expected effect.</p>	<p>Dendrochronological data can be used as a proxy for wind exposure by highlighting windthrow disturbances (e.g. Pettit and others 2021), but tree coring and laboratory analysis are time-consuming and thus costly.</p> <p>Lightning strikes creating scars in trunks are very rare stochastic events.</p>	
Tree density	LIDAR data	Using Bitterlich relascope or fixed-area plots	High for LIDAR; medium in the field	2 TreM groups potentially affected; the magnitude of expected effects is low to high, according to TreM types.	<p>Evaluating tree density requires multiple measurements in the field since trees are not regularly distributed.</p> <p>However, data is often available as the recording of TreMs is usually done at the same time as the stand measurement.</p>	Fairly bad	
Spatial distribution of the trees	LIDAR data	High precision GPS	High	1 TreM group potentially affected; the magnitude of expected effect is low.	Irrespective of the method used, recording accurate location of trees is always time-consuming and requires specific devices.	Bad	
Tree	Bark feature	From literature, at the tree-species level	Irrelevant	Low	3 TreM groups potentially affected; the magnitude of expected effects is low to high according to the TreM group.	Literature search needs only to be done once.	Good

Potential capacity to bear Mistletoe	From literature, at the tree-species level	Direct observation	Low	1 TreM group potentially affected; the magnitude of expected effect is high.	Mistletoe is actually a type of TreM and thus already routinely recorded.	Irrelevant
Phyllotaxis	From literature, at the tree-species level	Irrelevant	Low	1 TreM group potentially affected; the magnitude of expected effect is low to high, according to the TreM type.	Literature search needs only to be done once.	Fairly good
Proportion of heartwood vs sapwood	From literature, at the tree-species level	Irrelevant	Low	1 TreM group potentially affected; the magnitude of expected effect is low.	Literature search needs only to be done once. However, no data are available for most of the tree species.	Bad
Architectural models	From literature, at the tree-species level	Irrelevant	Low	1 TreM group potentially affected; the magnitude of expected effect is low.	Only informative for young trees or for conifers that develop without changing their morphology (e.g. <i>Abies</i> spp., <i>Picea</i> spp., <i>Pseudotsuga menziesii</i>). Indeed, during their adult stage, most tree species duplicate their initial architectural pattern to build the main branches of the crown (Barthélémy and Caraglio, 2007). The architectural diversity of adult crowns is, therefore, much lower compared to that of young trees (Chomicky and others 2017). Three main types of adult crowns can be distinguished: those of deciduous trees, those of conifers conforming to the initial pattern and those of the	Bad

					genus <i>Pinus</i> , which are intermediate between the two (Daina and Drénou 2021).	
Compartmentalization capacity	From literature, at the tree-species or tree-genera level	Irrelevant	Low	1 TreM group potentially affected; the magnitude of expected effect is high.	Literature search needs only to be done once. Compartmentalization capacity is available for a few species only (see Oven and Torelli 1999; Schneuwly-Bollschweiler and Schneuwly 2012; Gilman 2011; Dujesiefken and Liese 2015).	Fairly good
Physiological state	Remote sensing (Lambert et al. 2013)	Using the ARCHI method (Lebourgeois et al. 2015; Drénou et al. 2015)	Medium	4 TreM group potentially affected; the magnitude of expected effect is low to high according to TreM group.	Assessing physiological state would complement the results of studies that only compare snags and living trees. In the field, evaluating the physiological state of trees is challenging, since most methods are simply based on foliage discoloration and loss and do not take the resilience capacity of trees into account (Dujesiefken et al. 2005; Lambert et al. 2013). The ARCHI method (Lebourgeois et al. 2015; Drénou et al. 2015) is able to assess resilience capacity. However, it has to be developed for each tree species separately (Sabatier et al. 2014) and is currently available for only 15 species, including 7 broadleaves and 8 conifers (Joye 2019). The observer needs to be able to assess the top part of the tree crown from a distance (Lambert et al. 2013) which can become challenging in dense stands and in difficult conditions,	Fairly good

such as on steep slopes. Furthermore, few data are as yet available to assess the observer effect for the ARCHI status.
Remote sensing methods require particular skills and are still under development.

Age	Irrelevant	By tree-coring	High	2 TreM groups potentially affected; the magnitude of expected effect is low to high, according to the TreM group.	Tree-coring needs specific tools and materials, both in the field and at the laboratory. Furthermore, it needs skilled personnel to properly set a tree core. Tree-coring becomes especially challenging when the heartwood is already in an advanced stage of decay, which unfortunately occurs frequently in very large trees while these trees bear most of the TreMs.	Bad
Ontogenic stage	Irrelevant	By counting the main forks	Medium	7 TreM groups potentially affected; the magnitude of expected effect is low to high, according to the TreM group.	Require prior training (Drénou et al. 2020).	Good