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Running title: Formation of microhabitats on trees

Modelling the probability of microhabitat formation on trees using cross-sectional data

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Summary

1. Context: Tree-related microhabitats (TreMs), such as trunk cavities, peeled bark, cracks or sporophores of lignicolous fungi, are essential to support forest biodiversity because they are used as substrate, foraging, roosting or breeding places by bryophytes, fungi, invertebrates and vertebrates. Biodiversity conservation requires the continuous presence of TreMs in a forest. However, little is known about their dynamics. Moreover, we usually have only cross-sectional TreM data (observations of many trees at a single time), making it difficult to estimate TreM formation rates.

2. Method: This study adapted the methods of survival and reliability analysis to model the rate of TreM formation per unit of diameter increment as a function of tree diameter at breast height (DBH). We tested three variants of this model: the TreM formation rate independent of, proportional to or increasing non-linearly with DBH. We calculated the likelihood of the models, considering cross-sectional observations either of TreM presence/absence or TreM number on trees of different sizes. We calibrated the models in six sub-natural montane forests dominated by European beech *(Fagus sylvatica)* and silver fir *(Abies alba)* – in the French Pyrenees. Assuming an annual DBH increment value, the annual formation rate of TreMs was predicted both at the level of the tree and at the level of the forest stand.

3. Results: This method provided a coherent framework to model the probability that a TreM forms on a tree during a unit growth step and produces realistic predictions of TreM accumulation on trees. TreM formation accelerated as trees grew for *A. alba* but not for *F. sylvatica*. The TreM formation rate was twice as fast on *F. sylvatica* as on *A. alba*. We estimated a formation of 0.82–1.28 TreMs/ha per year and 0.5–0.9 TreM bearing trees/ha per year in the sub-natural forests studied.

4. Synthesis and applications: This method makes rigorous modelling of the formation of TreMs possible during the growth of trees and forest stands. The quantitative evaluation of

TreM fluxes will help to design forest biodiversity conservation strategies favouring the development and temporal continuity of TreMs.

Tweetable Abstract

The rate of TreM formation per unit diameter growth was modelled as a function of tree diameter at breast height (DBH), and the model was calibrated considering cross-sectional observations TreMs on trees of different sizes. The model predicted realistic TreM formation rates at the tree and stand levels in forests dominated by *Abies alba* and *Fagus sylvatica*. This approach opens new perspectives to the analysis of forest biodiversity conservation strategies.

1. Introduction

Forest ecosystems cover approximately 30% of the world's land surface (Pan *et al.*, 2013) and play a key role in terrestrial taxonomic biodiversity (Lindenmayer and Franklin, 2002). However, forest reserves account for only about 11% of the global forest area (Bollmann and Braunisch, 2013). Consequently, the conservation of forest biodiversity also depends on forests without a specific protection regime. The role of deadwood as a habitat for many insects, fungi or lichen species has been recognized for decades (Lachat *et al.*, 2013; Müller and Bütler, 2010; Seibold *et al.*, 2015; Gossner *et al.*, 2013; Speight, 1989; Stokland *et al.*, 2012; Bobiec *et al.*, 2005). More recently, research has focused on tree-related microhabitats (TreMs), which are singular morphological features developing on the trunks or branches of trees, such as cavities, cracks, peeled bark, root buttress concavities, epiphytes or sporophores

of saproxylic fungi. TreMs are used as substrate, foraging, roosting or breeding places by many species of taxa as diverse as lichens, bryophytes and fungi, micro-crustaceans, insects (e.g. Coleopterae, Dipterae, Hymenopterae), spiders, amphibia (e.g. *Anoura*, *Urodela*), birds (e.g. Picidae, Strigidae) and small mammals (e.g. Chiroptera, Gliridae, Mustelidae) (Stokland *et al.*, 2012; Winter and Möller, 2008). Some taxa are highly dependent on TreMs: more than 40% of birds in French forests use tree cavities or cracks for breeding (Blondel, 2005), and in Europe, roughly half of the insect species that breed in dendrothelms (i.e. water-filled holes) are strictly dependent on this habitat (Dajoz, 2007). TreMs are considered as relevant surrogates of direct biodiversity measures (Winter and Möller, 2008), particularly for saproxylic beetles (Bouget *et al.*, 2014; Bouget *et al.*, 2013), and are already integrated into some practical biodiversity assessment tools used by forest managers (Larrieu and Gonin, 2008). In addition, conservation of biodiversity in managed forests can be improved by protecting high-biodiversity-value trees such as trees bearing TreMs and dead trees from harvesting. This strategy, called the retention approach in forestry, appeared in the 1980s in the USA (Franklin *et al.*, 1981; Thomas *et al.*, 1979) and has aroused increasing interest in other parts of the word since then (Bütler *et al.*, 2013; Larrieu *et al.*, 2012; Lindenmayer et al. 2012; (Fedrowitz *et al.*, 2014). The idea first emerged as an alternative to clearcutting and is probably not sufficient to balance the impact of intensive logging on biodiversity. However, it is increasingly applied in selective harvest operations, where it is proposed as a means to integrate conservation into forest management (Gustafsson *et al.*, 2013). The retention of several high-biodiversity-value trees per hectare is therefore mandatory to obtain sustainable forest management certificates (FSC, 2016; PEFC, 2010).

TreMs are structures that form on trees during their development and disappear when the trees are harvested or die and decompose. It is therefore essential to quantify the TreM formation rate and compare it to tree mortality and tree harvesting rates in order to explain variations of TreM density in a forest stand. Several authors have shown that most TreM types are more frequent on snags, large living trees and broadleaved species (Larrieu and Cabanettes, 2012; Larrieu *et al.*, 2014a; Vuidot *et al.*, 2011). However, these results do not give direct indications on the rate of TreM formation on trees. Using a different approach, (Lindenmayer *et al.*, 1993) characterized the types and numbers of TreMs expected on trees of different life forms and diameters at breast height (DBH). On this basis, Ball *et al.* (1999) and Gibbons *et al.* (2010) developed a transition matrix model making it possible to simulate changes in forest structure, and therefore changes of TreM distribution. However, this approach relies entirely on the estimation of transition probabilities between life forms, a point little described by the authors. A simple way to estimate a TreM formation rate would be to use the variations of TreM number on trees observed repeatedly. Unfortunately, such repeated TreM measurements are still largely missing because of the relatively recent interest researchers have taken in this subject (Lindenmayer *et al.*, 2011). Moreover, trees have rarely been labelled in the field in previous studies, making new measures on the same trees impossible. TreM types such as woodpecker holes are rare and the detection of their formation requires large tree samples (Larrieu *et al.*, 2014a). Huge measurement efforts will be necessary before large databases with repeated observations of TreMs are available.

Inferring the rate of TreM formation from cross-sectional data (observation of several individuals representing different development stages) is required because of data availability. However, this poses several challenges. First, we usually do not know the age of trees. It is therefore difficult to relate TreM formation to a time scale. Second, observations

are censored: we do not know exactly at what time the TreM formation event has occurred or will occur. If we observe a TreM on a tree, we only know that the formation of the TreM occurred before the time of observation (this is called left censoring). New TreMs will perhaps form on the tree in the future, but we do not know when (this is called right censoring). Survival analysis and reliability analysis are other fields of research challenged by modelling the occurrence of events during the development of a population. These techniques analyse the expected duration of time until one or more events occur, such as death in biological organisms and failure in mechanical systems, and the rate of these events (Hosmer *et al.*, 2008; Meeker and Escobar, 1998). They answer questions such as: what is the proportion of a population which will survive past a certain time? Of those that survive, at what rate will they die or fail? How do particular circumstances or characteristics increase or decrease the probability of survival?

The objective of this study was to test whether we could transpose the concepts of survival and reliability analysis to model the event of TreM formation on trees and apply it to cross-sectional data. We considered that the test would be successful if this approach provided a logical and coherent framework for the analysis of the data as well as good predictions. We also tested three biological hypotheses. The first hypothesis postulates that TreM formation accelerates during tree growth, in relation to the observation of a disproportionate proportion of TreM bearing trees among large trees (Larrieu and Cabanettes, 2012). The second one advances that the rate of TreM formation is higher on broadleaved than conifer trees of similar size, in agreement with the observation of a higher frequency of TreM-bearing trees on broadleaf trees (Larrieu and Cabanettes, 2012). The third one hypothesizes that at the stand level, the rate of TreM formation is not strongly correlated to TreM density, meaning that the dynamic and the static perspectives are complementary. We applied the survival

analysis approach to TreM cross-sectional observations coming from mixed sub-natural forests in the Pyrenees dominated by a broadleaved species, European beech (*Fagus sylvatica*) and a coniferous species, silver fir (*Abies alba*). These two tree species are important late successional species in Europe and have a great economic and ecological importance. Moreover, tree architecture, microhabitat density, wood decay rate and biocenosis differ substantially between broadleaves and conifers (Larrieu *et al.*, 2014b).

2. Material and methods

2.1. Data

The data (Larrieu, 2017) were recorded in six forests unmanaged for more than 100 years located in the central Pyrenees mountain range (Lat: 42°45′N-43°3′N – Long: 0°9′W-0°36′E), at the montane altitude level (900– 1750 m). Observations were made in the summers of 2008 and 2009 (Larrieu *et al.*, 2012) on 37 circular plots with random locations within areas defined by their accessibility. We used the constant angle method (Bitterlich, 1984) in order to increase the proportion of large trees in the sample and obtain a better balance between observations of small and large trees and a better balance between observations of trees with and without TreMs in the data set. Trees above 2.5 cm DBH were observed when the ratio between their DBH and the distance to the center of a plot was more than 1/50. The radius R_i of the sampled area therefore increased as tree size increased ($R_i = 50DBH_i$). For stand level applications, we weighted each tree depending on the area sampled for its DBH. For each tree, the DBH outside the bark, the species of the tree and all the TreMs on the trunk beneath and within the tree crown were recorded, in reference to a list of seven TreM types: (i) cavities whose entrance was wider than 3 cm, (ii) missing bark area covering at least 100 cm^2, (iii) cracks in the trunk 1–5 cm wide, (iv) dendrothelms greater than 3 cm wide at the entrance, (v) sporophores of saproxylic fungi (polypores and pulpy agarics), (vi) epiphytes

(Yvi and foliose lichens) and (vii) dead-wood in the crown. Every tree was observed on all sides, from its foot and from a distance of dozens of meters using binoculars, to make as exhaustive an observation as possible. The data set was composed of 891 *A. alba* trees, 248 *F. sylvatica* trees and 110 trees of other broadleaved species, each of which was represented by fewer than 35 individuals (*Buxus sempervirens*, *Betula pubescens*, *Sorbus aucuparia*, *Tilia platyphyllos*, etc.). Five hundred trees had at least one TreM and 749 trees had no TreMs. Since several TreM types were recorded less than ten times per species, we considered that the data set was too small for a detailed analysis and we grouped all the TreMs in a single type and all species other that *A. alba* and *F. sylvatica* in a single group. We also used DBH increment records of the French National Forest Inventory in the "High Pyrenees" ecological region between 900 m and 1750 m elevation (sample of 757 *A. alba* trees and 2105 *F. sylvatica* trees), reaching a rough estimate of the annual DBH increments of the trees in the data set of 2.34 mm/year for *F. sylvatica* (SD=1.7 cm), 3.74 mm/year for *A. alba* (SD = 2.73 cm) and between 1.11 mm/year (*Crataegus monogyna*) and 4.96 mm/year (*Acer platanoides*) for the other species

2.2. Adaptation of the survival analysis approach to the formation of the first TreM

Scientists practicing survival or reliability analysis process the time to an event as a random variable (Hosmer *et al.*, 2008; Meeker and Escobar, 1998; Clark, 2007). This event is usually the death of an individual or the failure of a machine. We considered the event of interest as the formation of a TreM. Survival and reliability analyses are usually performed on repeated measures describing the development of a cohort of individuals observed several times. Having only cross-sectional observations of trees of different DBHs, we replaced time with DBH in the analysis. However, this implies the assumption that TreM bearing trees had a similar rate of mortality than other trees during their growth (see 4.4.).

Let us define D as a random variable corresponding to the DBH of a tree when it contracts its first TreM. Following the survival analysis theory, we can define five related functions:

$S(d)$ is the probability that no TreM forms on a tree before it grows to diameter d. This is analogous to a survival function (probability of still being alive when reaching age t).

$$S(d) = Pr\{D > d\} \quad \text{(eq. 1)}$$

$F(d)$ is the probability that the first TreM forms on a tree before it grows to diameter d. $F(d)$ is the cumulative distribution function (CDF) of the random variable D. *F(d)* can also be interpreted as the probability that a tree observed at diameter d carries at least one TreM. This interpretation means that it is possible to estimate *F(d)* with our data.

$$F(d) = Pr\{D \leq d\} = 1 - S(d) \quad \text{(eq. 2)}$$

$f(d)$ is the probability density function of the random variable D or event density. The function *f(d)* describes the distribution of DBHs at which the first TreM appears on the trees of a population. If F is differentiable,

$$f(d) = \lim_{\partial d \to 0} \frac{Pr\{d \leq D \leq d + \partial d\}}{\partial d} = \frac{\partial (F(d))}{\partial d} \quad \text{(eq.3)}$$

$h(d)$ is the hazard rate, defined as the rate of formation of the first TreM at diameter d, on condition that the tree has contracted no TreM before (that is, $D \geq d$). The hazard function h(d) deserves special attention because it directly describes the process of TreM formation and how this process changes during diameter growth.

$$h(d) = \lim_{\partial d \to 0} \frac{Pr\{d \leq D \leq d + \partial d \ / \ D \geq d\}}{\partial d} = \frac{f(d)}{S(d)} \quad \text{(eq.4)}$$

H(d) is the cumulative hazard function, describing the "accumulation" of the hazard over growth.

$$H(d) = \int_0^d h(x)dx = -Ln(S(d)) \quad \text{(eq. 5)}$$

These five functions are closely related but provide complementary descriptions of the relation between TreM formation and tree DBH. We will see below that *F(d)* is especially useful to estimate the parameters of the model, whereas *h(d)* provides the more direct description of the TreM formation process and *H(d)* is used in discrete time simulations.

2.3. The Weibull family of functions used to model a monotonic change of hazard with DBH

Survival analysis theory has identified efficient parametric functions that lead to interpretable forms of the hazard function *h(d)*. The most classical form for *f(d)* is the Weibull function with two parameters: a shape parameter *k* and a scale parameter *λ*. If *f(d)* is a Weibull distribution, the hazard function is simply a power function of DBH. The functions are written as follows:

$$\forall (\lambda, k) \in (\mathbb{R}_+^*)^2$$

$$S(d) = e^{-\left(\frac{d}{\lambda}\right)^k} \quad \text{(eq. 7)}$$

$$F(d) = 1 - e^{-\left(\frac{d}{\lambda}\right)^k} \quad \text{(eq. 8)}$$

$$f(d) = \frac{k}{\lambda}\left(\frac{d}{\lambda}\right)^{k-1} e^{-\left(\frac{d}{\lambda}\right)^k} \quad \text{(eq.9)}$$

$$h(d) = \frac{k}{\lambda^k} d^{k-1} \quad \text{(eq.10)}$$

$$H(d) = \frac{d^k}{\lambda^k} \quad \text{(eq.11)}$$

If k = 1, the hazard is constant and does not depend on DBH. This might suggest random external events are causing TreM formation. In that case, *f(d)* reduces to an exponential distribution.

If $0 < k < 1$, the hazard declines as DBH decreases.

If k>1, the hazard rises as DBH increases. This means that trees without any TreM become increasingly susceptible to contracting their first TreM during an infinitesimal growth step as their DBH increases. The corresponding process is called "ageing" in survival theory and corresponds to a maturation process in this example. If k=2, hazard increases proportionally with increasing DBH. In that case, *f(d)* reduces to a Rayleigh distribution.

Summary statistics can be calculated for D. If *f(d)* is a Weibull, E(D) and Var(D) are related to a gamma function. The median of the expected D at which the first TreM forms is expressed simply as:

$$M(D) = \lambda(Ln2)^{\frac{1}{k}} \quad \text{(eq.12)}$$

2.4. Formation of successive TreMs

If we assume as a first approximation that the formation of TreMs during an interval of time is influenced by neither the presence/absence of a previous TreM nor the number of previous TreMs on the same individual, the formation of successive TreMs is a Poisson stochastic point process (Meeker and Escobar, 1998; Rausand and Hoyland, 2004). The probability of formation of n TreMs during tree growth to DBH d is:

$$Pr[N(d) = n] = Pois(\mu(d)) \quad \text{(eq. 13)}$$

$\mu(d)$ is the expected number of TreMs at DBH d:

$$\mu(d) = E[N(d)] \quad \text{(eq. 14)}$$

$\nu(d)$ is the recurrence rate of TreM formation, assuming that $\mu(d)$ is differentiable,

$$\nu(d) = \frac{\partial \mu(d)}{\partial d} = \frac{\partial E[N(d)]}{\partial d} \quad \text{(eq.15)}$$

In a Poisson point process, the recurrence rate $\nu(d)$ is equal to the hazard rate $h(d)$ of formation of the first TreM, and the expected number of TreMs $\mu(d)$ is equal to the cumulative hazard $H(d)$ (Rausand and Hoyland, 2004).

2.5. Model calibration

We tested two approaches for model calibration. We considered first the binary variable corresponding to the presence (y_i=1) or absence (y_i=0) of at least one TreM on tree i. The likelihood function of a set of parameter values (k, λ) given the observation of TreM presence/absence on a single tree of DBH d_i is equal to a Bernoulli probability distribution with a success probability of $F(d_i; k, \lambda)$. If we assume that TreMs form independently on different trees, the likelihood of a set of parameter values (k, λ) given the observations of TreM presence/absence on N trees is:

$$L(k, \lambda) = \prod_{i=1}^{N} Ber(y_i \,| F(d_i; k, \lambda)) \quad \text{(eq.16)}$$

We then considered the count variable corresponding to the number of TreMs n_i observed on tree i. The likelihood function of a set of parameter values (k, λ) given the observation of n_i TreMs on a single tree of DBH d_i is equal to a Poisson probability distribution with a mean of $\mu(d_i) = H(d_i; k, \lambda)$. If we assume that TreMs form independently on different trees, the likelihood of a set of parameter values (k, λ) given the observations of the distribution of trees having various numbers of TreMs in a set of N trees is:

$$L(k, \lambda) = \prod_{i=1}^{N} Pois(n_i \,| H(d_i; k, \lambda)) \quad \text{(eq.17)}$$

We tested three hypotheses concerning the shape of the hazard rate function h(d) and the probability density function f(d) (i) Hypothesis 1: k=1, $h(d)$ is independent of d and f(d) is an Exponential distribution function. (ii) Hypothesis 2: k=2, $h(d)$ is proportional to d and f(d) is a Rayleigh distribution function. (iii) Hypothesis 3: k is a positive exponent to estimate, $h(d)$ is a power function of d and f(d) is a Weibull distribution function.

We fitted the three models on our data set with a Bayesian approach using the "runjags" package (Denwood, 2016) in the R software (R Development Core Team, 2005). The code is provided in Appendix 1. We combined all the trees of the six forest sites without modelling any site effect. For the three models, we chose the parameter λ to be a gamma prior distribution with a mean of 100 and a variance of 500: $\lambda \sim \Gamma(\text{shape} = 20, \text{rate} = 0.2)$. For the Weibull model, we chose the parameter k to be a gamma prior distribution with a mean of 2 and a variance of 4: $k \sim \Gamma(\text{shape} = 1, \text{rate} = 0.5)$. For each model, three Monte Carlo Markov (MCMC) sampling chains of 10,000 values were used with the first 1000 values as the warm-up stage. We checked MCMC convergence using the $\hat{R}$ criteria (Gelman et al. 2013).

2.6. Discrete-time simulation of TreM accumulation on trees and model evaluation

The application of the model depends on its use in simulations. In forest dynamics, simulations are usually made using a discrete time approach with annual time steps. If time steps are sufficiently short, we can assume that no more than one TreM can form during a time step. In this case the probability that a TreM forms on a tree during a time step (t, t+1) is:

$$P_{t,t+1} = \int_{d_t}^{d_{t+1}} v(d)\partial d = \int_{d_t}^{d_{t+1}} h(d)\partial d = H(d_{t+1}) - H(d_t) \quad \text{(eq. 18)}$$

If *f(d)* is a Weibull,

$$P_{t,t+1} = H(d_{t+1}) - H(d_t) = \frac{d_{t+1}^k}{\lambda^k} - \frac{d_t^k}{\lambda^k} \quad \text{(eq. 19)}$$

The model's capacity to represent the process of TreM formation on trees correctly was assessed by simulating the past growth of the trees in the data set from an initial DBH of 7.5 cm up to their current DBH and the accumulation of TreMs during this growth. For one prediction, we drew a vector (k, λ) in the MCM chains. For successive annual time steps, we calculated the initial and final DBH of the trees assuming constant increments equal to the National Forest Inventory mean DBH increment for the species in the study area. For each tree and each time step, the probability $P_{t,t+1}$ of formation of a TreM was calculated using equation (19), and a Bernoulli trial was conducted to determine whether or not to add a new TreM to the tree. At the end of the simulation, we calculated the predicted proportion of trees carrying at least one TreM per DBH class of 10 cm, and the predicted proportion of trees carrying zero to six TreMs in the population. We replicated the simulations 1,000 times and obtained a distribution of 1000 predicted values of proportions of trees carrying at least one or zero to six TreMs. We then calculated 95% intervals of these predicted values, to compare predictions and observations.

For each type of prediction, we calculated a set of three predictive loss criteria proposed by (Gelfand and Ghosh, 1998). This approach is based on the calculation of a goodness-of-fit measurement G_m characterizing the distance between the predicted values and the observed value, and a penalty term P_m characterizing the variance of the predictions. The best model is the model with the lowest values for these criteria. This approach makes it possible to compare both nested and non-nested pairs of models and responds to model over- or under-

fitting without requiring the arbitrary choice of a penalty depending on the number of parameters.

$$G_m = \sum_{i=1}^{N} \frac{\left(y_{obs_i} - \overline{y_{pred_i}}\right)^2}{N} \qquad \text{(eq. 20)}$$

$$P_m = \sum_{i=1}^{N} \frac{V(y_{pred_i})}{N} \qquad \text{(eq. 21)}$$

$$D_m = G_m + P_m \qquad \text{(eq. 22)}$$

y_{obs_i} is the observation for tree i in the data set, $\overline{y_{pred_i}}$ is the mean of the predictions for tree i over simulation replications and $V(y_{pred_i})$ is the variance of these predictions.

2.7. Application: predicting the rate of TreM formation at the forest stand level

To analyse the rate of formation of TreMs at the stand level, new simulations were carried out using the observed DBH of each tree in the data set as an initial state. For this section, only the Rayleigh model was used because of its good predictive performance and simplicity (see § 3.2.). We sampled 1000 estimates of parameter λ in the MCM chain and made 1000 predictions of TreM formation during an annual diameter increment for each tree. Taking into account the sampling area corresponding to the DBH of each tree (constant angle sampling method, see § 2.1.), we calculated a predicted distribution of TreM formation rates per year and per hectare for each of the six forests. We then used linear regression to analyse the relation between the forest's TreM formation rate and the forest's TreM density or TreM bearing tree density.

3. Results

3.1. Relationship between TreM formation rate and tree diameter

Model calibration using the observation of the presence/absence of TreMs (likelihood function (16)) or the observation of the number of TreMs on trees (likelihood function (17)) gave very close results. We present the detailed results of the first method for the two dominant species (*F. sylvatica* and *A. alba*) in the main text and figures and provide the results of the second method in Appendix 2.

$\hat{R}$ criteria values (Gelman et al. 2013) were less than 1.1, revealing a good convergence of the MCMC chains for the three models: Exponential, Rayleigh and Weibull. Uncertainties were reasonably small, as shown by the credible intervals of the parameters (Table 1) and the confidence envelopes of the functions h(d), F(d) and f(d) (Figure 1). Higher values of λ for *A. alba* than *F. sylvatica* (Table 1) translated into lower TreM formation rates for *A. alba* than *F. sylvatica* at all diameters and for all models (Figure 1). The TreM formation rate for *A. alba* was for example only one-third of that for *F. sylvatica* in the Rayleigh model. The median expected diameter D at which a tree contracts its first TreM was therefore higher for *A. alba* than *F. sylvatica*: 88 cm [79–98] for *A. alba* (median and 95% confidence interval of the 1000 medians of D calculated over 1000 simulations) and 35 cm [30–42] for *F. sylvatica* with the Exponential model, 74 cm [70–78] for *A. alba* and 45 cm [41–49] for *F. sylvatica* with the Rayleigh model, 73 cm [66–82] for *A. alba* and 42 cm [34–50] for *F. sylvatica* with the Weibull model. These figures also show that the expected DBH of the first TreM formation estimated by the Rayleigh and Weibull models were quite similar and contrasted with the values estimated by the Exponential model. Uncertainties were higher for the group of diverse species, probably because of differences in growth and TreM formation rates among this group's species. However, the parameter estimates were reasonable and rather close to the values for *F. sylvatica*.

The shape of the hazard function h(d), which describes how the TreM formation rate changes with tree DBH d, differed strongly among models (Figure 1). By construction, h(d) did not depend on d in the Exponential model. In contrast, h(d) increased linearly as d increased in the Rayleigh model and showed a divergence between *F. sylvatica* and *A. alba* at higher. The Weibull model was more flexible because of the combination of two parameters k and λ. The hazard rate h(d) of the Weibull model increased almost linearly with d for *A. alba*. However, for *F. sylvatica*, the hazard rate increased non-linearly as d increased because of a mean estimate of 1.6 for parameter k, i.e. an exponent of $k - 1 = 0.6$ in the relation h(d). Because of this non-linearity in the Weibull model, the differences in hazard rate between the two species were maximum at medium values of d and then diminished for larger trees (Figure 1).

3.2. Models' capacity to simulate the process of TreM formation

For *A. alba*, the predictive loss criteria of the proportion of TreM bearing trees per DBH class indicated a lower performance of the Exponential model compared to the Rayleigh and Weibull models (Table 2). For *F. sylvatica*, the three models showed a comparable performance. A graphical analysis (Figure 2) showed that this poor performance of the Exponential model for *A. alba* came from a prounced underestimation of the proportion of TreM bearing trees at huge DBHs, revealed by a discrepancy between the predictive envelopes and the data points. The correspondence between the predictive envelopes of the Rayleigh or Weibull models was more satisfying despite several data points slightly outside of the envelopes. For *F. sylvatica* the observations themselves did not show a clear pattern, especially in classes of large DBHs represented by a few individuals. The three models nevertheless managed to predict medians that increased monotonously as DBH increased and predictive envelopes covering most data points.

For both species, the predictive loss criteria of the proportion of trees in classes of zero to six TreMs did not distinguish the performance of the three models (Table 2). The graphical analysis (Figure 3) showed, however, that the three models slightly overestimated the proportion of *A. alba* without any TreM and slightly underestimated the proportion of *A. alba* with a single TreM. For *F. sylvatica*, the three models underestimated the proportion of trees with one or two TreMs and slightly overestimated the proportion of trees with three TreMs or more.

Together, the tests identified the Rayleigh model as a good compromise between performance and simplicity for *A. alba*. The two models simulating an increase of the rate of TreM formation with DBH over-performed the model simulating a constant rate of TreM formation for this species. For *F. sylvatica*, the three models gave comparable results. The best compromise between performance and simplicity could therefore be the Exponential model, simulating a constant TreM formation rate during tree growth.

3.4. TreM formation at the stand level

The individual probability of annual TreM formation was 0.52% chances per year [0.15%−0.98%] (median and 95% predictive interval) for *A. alba* trees and 0.95% chances per year [0.31%−1.69%] for *F. sylvatica* trees in the forests studied. The mean predicted rates of TreM formation at the stand level varied from 0.82 to 1.28 TreM per ha and year depending on the forest (Table 3). This number could be multiplied by up to five in some simulations because of the uncertainty about the estimate of parameter lambda and of the stochasticity of the Bernouilli trials. These mean predicted rates of TreM formation corresponded to 0.47–0.69 TreMs per year for 100 trees larger than 17.5 cm, 1.48–2.43 TreMs per year for 100 TreM

bearing trees or 1.04–1.99 TreMs per year for 100 TreMs already present. The time required to reconstitute the TreMs present in the stands can be estimated as the inverse of the latter rate: between $100/1.99 = 50$ years and $100/1.04 = 96$ years. The predicted rates of new TreM bearing tree formation (i.e. trees receiving their first TreM) varied from 0.5 to 0.9 new TreM bearing trees/ha per year.

The regressions between the TreM formation rate at the stand level and the density of TreMs or the density of TreM bearing trees showed that only these two co-variables were not capable of explaining the differences of TreM formation rates among forests (non-significant effects at a level of 5%).

4. Discussion

4.1. Survival analysis provides a change of perspective for TreM studies

Our adaptation of the survival and reliability theory appeared to be an efficient framework for the modelling of TreM formation. This approach made it possible to calibrate the relationship between the TreM formation rate and the DBH of a tree using cross-sectional data. Discrete time simulations of tree growth and TreM formation produced good predictions of the resulting distribution of TreMs in our forests.

This approach brings a key change of perspective in the study of TreMs. Most previous studies have concentrated on analysing the distribution of TreMs in a forest from a static perspective. Generalized linear models based on Poisson distributions have been used to analyse the number of TreMs of a given type on trees (Lindenmayer *et al.*, 1993) or the number of TreM types per tree (Vuidot *et al.*, 2011; Larrieu *et al.*, 2014a). Logistic models have also been used to analyse the presence/absence of different TreM types on trees (Larrieu *et al.*, 2014a; Vuidot *et al.*, 2011). These studies did not connect the distributions of TreMs observed at a given time to the dynamic process that generates them, even though they could

have done so by considering their models as the cumulative distribution function of a TreM formation process. In contrast, our approach focuses on the estimation of the TreM formation rate and the simulation of TreM accumulation during tree growth. Herein, we concentrated on Weibull family models because they represent the hazard rate with a simple power function of DBH, making it easy to test the three basic hypotheses: that the hazard is independent, continuously decreasing or continuously increasing with DBH. Other distributions defined in $\mathbb{R}^+$ have been proposed as probability density functions in survival and reliability analyses, such as the Gompertz, the gamma, the logistic, the generalized gamma, the log-normal, the log-logistic, etc. (Meeker and Escobar, 1998). They lead to more complicated and less flexible hazard functions. Moreover, they often lead to predictions very close to those made with a Weibull model. It is recommended to use these more complex functions only when they are justified by prior knowledge of the shape of the hazard function (Hosmer *et al.*, 2008). We therefore started with the most simple hazard function in this methodological paper.

4.2. The relationship between TreM formation and tree growth depends on tree species.
Several earlier studies showed that the presence and number of TreMs on a tree are related to its diameter and species (Larrieu and Cabanettes, 2012; Vuidot *et al.*, 2011; Winter *et al.*, 2015). Moreover, Larrieu and coauthors (Larrieu and Cabanettes, 2012; Larrieu *et al.*, 2012) observed a disproportionate abundance of TreMs on very large trees. The better performance of the Rayleigh and the Weibull models over the exponential model for *A. alba* supports the idea that the TreM formation rate increases as DBH increases, i.e. that TreM formation accelerates during tree growth. This seems sound from an ecological point of view given that events such as breakings of large branches or cavities made by nesting birds should occur with a higher probability on large trees. However, for *F. sylvatica*, the three models gave

comparable results. The acceleration of TreM formation during tree growth is therefore not clear for this species. This acceleration could also be an artefact if TreMs influence tree mortality in such a way that small trees with TreMs die faster than large trees with TreMs. We obtained clearly higher estimates of TreM formation rates for *F. sylvatica* than for *A. alba*. This result is in agreement with previous authors (Larrieu *et al.*, 2012; Vuidot *et al.*, 2011), who observed that there were more TreMs on *F. sylvatica* trees than on fir trees of the same diameter. They also showed that cavities, missing bark and dendrothelms were mainly associated with *F. sylvatica*, whereas more diverse TreM types were found on *A. alba*. This difference in TreM types could explain the differences in the shape of the relationship between hazard rate and DBH that we found between these two species. Studies on more species are needed to explore the generality of these results. We expect that a difference between broadleaved and coniferous species will remain rather consistent because they have different crown architectures and different bark and wood properties: broadleaves have more large branches prone to breakage and more branch forks, usually have a thinner bark and their wood decomposes much faster, all phenomena facilitating faster development of TreMs such as cavities. Moreover, in this study, the parameter values obtained for the group of diverse broadleaved species was much more similar to values obtained for *F. sylvatica* than for *A. alba*.

4.3. TreM dynamics as an indicator of potential biodiversity change

Our prediction of a formation of 0.82–1.28 TreMs per ha and year gives an order of magnitude for temperate montane mixed forest stands with a high degree of maturity. However, this figure represents only TreMs formed on living trees and should be complemented by TreMs formed on standing dead trees (Larrieu and Cabanettes, 2012). TreM formation in managed stands should be lower because of a reduction of large trees,

dead trees, and a tendency of forest managers to eliminate trees with TreMs negatively impacting wood quality (Larrieu *et al.*, 2012). However, TreMs such as missing bark areas and dendrothelms can also increase because of harvesting (Larrieu *et al.*, 2014a; Larrieu *et al.*, 2012) if trees are damaged by the falling and logging of their neighbours.

The average formation of 1.04–1.99 new TreMs/year for 100 TreMs corresponds to 50–96 years required to reconstitute the TreMs of our stands. This result strengthens the idea that approximately 100 years without logging are necessary for a montane forest stand to acquire a structure comparable to a natural stand (Larrieu *et al.*, 2012). This roughly corresponds to one-third of the time necessary for a forest stand to complement a full sylvigenetic cycle (Larrieu *et al.*, 2014b).

Estimating a flux of TreMs completely requires balancing TreM formation with tree mortality and decomposition. The annual mortality rate of very large trees in temperate forests is usually less than 0.5% (Vieilledent *et al.*, 2010; Vieilledent *et al.*, 2009; Monserud and Sterba, 1999). This would correspond to a mortality of 0.24–0.4 TreM bearing trees/ha per year in our forests, compared to our prediction of 0.46–0.89 new TreM bearing trees/ha per year. Several types of TreMs can be considered as indicators of tree senescence (for example fungi sporophores) and it is probable that the mortality of trees carrying these TreMs is higher than the average. However, Larrieu *et al.* (2014b) showed that the availability of TreMs appears to be rather stable in unmanaged mountain mixed forests of different development stages, in terms of both quantity and diversity.

Neither the density of TreMs nor the density of TreM bearing trees was sufficient to predict the differences in the annual TreM formation rate between the sub-natural forests studied herein. This means that the presence of TreMs or TreM bearing trees does not guarantee a high TreM formation rate. This point is even more crucial in managed forests since forest management can shut down the formation of new TreM bearing trees despite the retention of

some old and large TreM bearing trees if the harvesting diameters are too low in the rest of the population. The tree retention approach alone therefore appears insufficient to maintain forest biodiversity over the long term. Senescence islands where a natural forest cycle can occur must also be preserved, and within managed areas a conservation strategy based on the functioning and the dynamics of the ecosystem is necessary. Indirect evaluations of forests' potential biodiversity are usually based on state variables such as TreM density or dead-wood volume observed at a given time (Larrieu and Gonin, 2008). Taking into account flux variables such as the TreM formation rate would empower these evaluations by providing an indication of the potential changes in biodiversity we can expect in the future.

4.4. Limits and perspectives

This study focused on the general applicability of survival analysis to the modelling of TreM formation. The good prediction capacity of the model used justifies the refinement of this approach and its extension to more complex situations. Certain assumptions were nonetheless simplified and must be kept in mind.

We treated cross-sectional observations of TreMs on trees of different DBHs as if they were longitudinal observations describing the accumulation of TreMs on a cohort of growing trees. This approach requires first that TreMs do not disappear on the trees, and second that the presence of TreMs does not modify the tree mortality rate. Some exceptions can be found to the first assumption: for example, a TreM corresponding to a small area of wood exposed after bark injury can be recovered by new bark and disappear. However, this type of situation is rare for the data set used in our study because the field protocol defined a minimum size of several centimetres for the TreMs to be recorded. The second assumption is also questionable because fungi, large cavities or crown dead wood are most often found on weak trees with a high probability of mortality. The results show that these two assumptions did not prevent

good model predictions in sub-natural forests. However, the approach should be used with caution in managed forests where forest managers may harvest TreM bearing trees more than the average because they consider them as low-quality trees or decaying trees, or less than the average because of their value for biodiversity (Larrieu *et al.*, 2014a).

We also assumed that a single model could represent the formation of TreMs of very different types. In the data set, cavities were the most widely represented TreM (35% of the total number of TreMs), followed by dead wood in the crown (25%), epiphytes (20%) and missing bark (14%). Cracks and sporophores accounted for a tiny proportion (around 3% each) of the TreMs. All these TreMs share essential properties: they usually are small, discrete ecological objects, whose formation starts rather suddenly and that depend on the maturation of a tree. The results indicate that modelling them together provides reasonable predictions at the tree and stand levels. Pooling them seems warranted in this methodological paper. In addition, modelling them together is consistent with integrative approaches of forest biodiversity that consider the whole group of TreMs as a key forest structure dimension influencing biodiversity, as a complement to other dimensions such as dead wood, tree species diversity, size inequality and spatial distribution, or understory vegetation (Stokland *et al.*, 2012; Larsson, 2001; Kraus and Krumm, 2013). Thinking of TreMs as a group helps to discuss conservation strategies that can be generalized beyond specific case studies. However, modelling the formation of each TreM type separately is an important perspective for future work. This is especially relevant given that different TreM types do not have the same density at the stand level, do not host the same taxa and do not have the same importance for biodiversity conservation in terms of species richness or threat status of hosted species. Woodpecker breeding cavities are, for example, particularly crucial to protect because they are rare and play a key role for the woodpecker itself but also for other cavity

nesting birds, bats, many arthropods, etc. Moreover, not only the quantity but also the diversity of TreM types is important for biodiversity conservation (Bouget *et al.*, 2013). The modeling of the formation of individual TreM types will require, however, a large data set to provide enough observations of rare TreM types. From the modelling point of view, the use of different probability density functions may also be required to describe the differences of formation processes among TreM types.

In the estimation based on the number of TreMs observed on trees and in the simulations, we assumed that TreM formation was a Poisson point process, i.e. the formation of a new TreM was independent of the presence of TreMs on a tree. Similarly, we assumed independence among neighbouring trees. The calibration made on the observation of TreM presence/absence and the calibration made on the observation of the number of TreMs on trees produced very close parameter estimates. This stems from the fact that 90% of the *A. alba* and 70% of the *F. sylvatica* had 0 or 1 TreM. Taking into account the number of TreMs observed therefore did not contribute much additional information. The accuracy of our predictions validates the assumption of a Poisson point process for *A. alba* but is more questionable for *F. sylvatica*. Some TreMs may prepare the formation of another TreM on the tree. For example, several studies have shown that cavities often appear after sporophore emergence (Cockle *et al.*, 2012) since woodpeckers can dig their nesting holes more easily in altered wood (Cramp, 1989). Larrieu *et al.* (2012) and Winter *et al.* (2015) also showed different co-occurrences between TreM types. The presence of TreMs on the subject tree or on its neighbours could indeed be considered as a co-variable potentially influencing the probability of appearance of a new TreM. Last, some TreMs may evolve into another TreM type. For example, an area of exposed wood may evolve into a cavity colonized by saproxylic fungi and insects. In that case the appearance of a new TreM should be combined with the

disappearance of its predecessor and a model of TreM succession would be required. Our results show that neglecting these processes was reasonable when TreM types are pooled together. However, they should be considered when analysing the dynamics of different TreM types more precisely. The elaboration of more complex approaches describing temporal successions of TreM types therefore constitutes an interesting challenge for future research.

Another research perspective is the introduction of a site effect or explicit co-variables describing site conditions (fertility, slope, rock falls, wind hazard, etc.) in the model. Substantial differences in TreM density have been shown for example between Mediterranean, montane and lowland forests (Bouget *et al.*, 2014; Regnery *et al.*, 2013; Remm *et al.*, 2006; Vuidot *et al.*, 2011). These effects could partly be explained by methodological differences among studies but have also been reported by authors analysing a range of sites in a single study (Bouget *et al.*, 2014; Vuidot *et al.*, 2011).

All these perspectives require large data sets. TreM data have been gathered by authors in several countries (France, Germany, Ukraine, Sweden, Switzerland, the United States, Canada and Australia), and the constitution of collaborative databases is a key to future progress.

As the interest in TreMs increases, repeated observations on permanent plots should become available in the future (Lindenmayer *et al.*, 2011). These data will make it possible to directly validate the TreM formation rates estimated with our approach and to better identify the drivers of TreM dynamics. However, repeated observations will always remain much rarer than cross-sectional observations and methods making the most of both types of observations will remain essential.

With simulation studies Ball *et al.* (1999) and Gibbons *et al.* (2010) have shown that forest management can drastically modify the availability of TreMs in a forest. With the approach presented in this study, we propose a more robust and general modelling framework for this kind of research. We are currently in the process of implementing our TreM formation model in the individual-based forest dynamics simulator Samsara2 (Courbaud *et al.*, 2015). The user can define a wide range of silviculture strategies in Samsara2 by defining silviculture controls such as the time between cuttings, the volume harvested, the limit cutting diameter and conservation options such as the number of large trees and the percentage of dead-tree volume to retain. Simulation experiments can then be conducted by varying the levels of these controls among modalities (Lafond *et al.*, 2015; Lafond *et al.*, 2017; Lafond *et al.*, 2014). Implementing a TreM formation model in Samsara2 will make it possible to test more precise conservation strategies such as retention of TreM bearing trees and to analyse their effect on the dynamics of TreMs in forest stands over long time periods.

Other types of discrete events occurring during the life of living organisms can be studied using survival and reliability theories. In medicine, survival analysis is often used not only to model the risk of death, but also to model the risk of contracting a disease (Hosmer *et al.*, 2008). Disease, injuries, parasite attacks, predation, ontogenic changes, etc., can be thought of as ecological processes that could be studied with this type of approach. As discussed above, the adaptation of survival and reliability methods to the use of cross-sectional data requires additional assumptions (the results of the event still visible on the individuals, no effect of the event on individual mortality). It is therefore better to use survival and reliability theory as much as possible in its original context of the longitudinal study of a cohort of individuals and to reserve the use of cross-sectional data to well-identified cases.

Conclusion

This study showed that survival and reliability theory provides a strong framework to model the probability of TreM formation at both the tree and stand levels. The use of cross-sectional data for model calibration led to reasonable parameter estimates and predictions. This approach opens interesting perspectives for the understanding of the TreM formation process and for the design of forest biodiversity conservation strategies favouring the development and temporal continuity of TreMs.

Data accessibility:

Data: Dryad Digital repository http://dx.doi.org/10.5061/dryad.h85q3

Author contributions statement:

BC and CP conceived the ideas, designed methodology and analysed the data; LL and AC collected the data; AL contributed to the theoretical justification of the approach. BC, CP and LL led the writing of the manuscript. All authors contributed critically to the drafts and gave final approval for publication.

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Supporting information:

TreMFormation.Appendix1.r: R code to estimate TreM formation rate using cross-sectional observations of TreM presence or TreM number on trees.

TreMFormation.Appendix2.pdf: Results of the parameter estimation and model evaluation with the Poisson point process approach.

Tables

Species	Model	Parameter	Lower95	Median	Upper	DIC
Abies alba	Exponential.PP	λ	113.17	126.65	141.21	1003
	Rayleigh.PP	λ	83.64	88.46	93.88	960
	Weibull.PP	λ	81.10	87.48	94.69	962
		k	1.73	2.07	2.43	
Fagus sylvatica	Exponential.PP	λ	42.97	50.83	59.57	589
	Rayleigh.PP	λ	49.65	53.94	58.80	604
	Weibull.PP	λ	46.89	52.91	58.76	590
		k	1.12	1.63	2.15	
Diverse sp.	Exponential.PP	λ	43.85	61.16	83.18	108.8
	Rayleigh.PP	λ	31.83	38.69	46.35	NaN
	Weibull.PP	λ	34.19	59.94	101.08	NaN
		k	0.51	1.01	1.70	

Table1

Species	Model	Habitat trees / DBH class			Trees / Nb of TreMs		
		Gm	Pm	Dm	Gm	Pm	Dm
Abies alba	Exponential	0.055	0.029	0.084	0.004	0.000	0.005
	Rayleigh	0.008	0.007	0.016	0.002	0.000	0.002
	Weibull	0.008	0.007	0.015	0.001	0.000	0.002
Fagus sylvatica	Exponential	0.010	0.009	0.018	0.001	0.001	0.001
	Rayleigh	0.014	0.004	0.018	0.005	0.000	0.006
	Weibull	0.011	0.005	0.017	0.004	0.001	0.005

Table 2:

Forest name	BURAT	BOIS NEUF	CAUTERETS	BARADA	ES PICHES	PLAGNET DE TON
Tree density (no.ha^{-1})	254.96	210.80	118.05	264.44	181.00	231.17
Basal area (m^{2}ha^{-1})	28.20	32.59	29.99	43.52	30.01	32.01
Arithmetic mean DBH (cm)	33.63	40.24	52.88	42.08	42.52	37.70
Mean annual DBH increment (mm.year^{-1})	3.41	3.40	3.78	3.55	3.45	3.11
Proportion of *Abies alba* trees	0.74	0.69	0.89	0.87	0.79	0.53
Habitat-tree density (no.ha^{-1})	49.09	78.14	42.25	64.94	52.24	81.11
TReM density (no.ha^{-1})	59.91	111.10	52.05	75.96	63.60	108.49
Mean TReM production (no.ha^{-1}year^{-1})	1.19	1.16	0.82	1.15	0.87	1.28
Mean habitat-tree prod. (no.ha^{-1}year^{-1})	0.89	0.63	0.46	0.83	0.52	0.55

Table 3

Figure captions:

Table1: Summary of posterior parameter estimates for the three TReM formation models.

Table 2: Predictive loss criteria comparing the predictions and observations of the proportion of habitat trees in each DBH class and the proportion of trees with zero to six TreMs in the data set.

The criteria were calculated on 1000 predictions of the numbers of TReMs carried by the trees in the data set for the different species and models. A prediction was made by simulating the growth of each tree from a DBH of 5 cm up to its current DBH and the related formation of TreMs at each time step. Gm represents the distance between predictions and observations, Pm represents the prediction uncertainty, and Dm is the sum of the two. The lower the values of these criteria, the better the model performs.

Table 3: Characteristics of the six forests of the data set and predictions of the annual TreM formation and TreM bearing tree formation rates.

Figure 1: Characteristic relationships for the three models of TreM formation.

The function $f(d)$ is the probability density function of the random variable D, corresponding to the diameter at which a tree contracts its first TreM. $F(d)$ is the cumulative distribution function of the random variable D and corresponds to the probability that at least one TreM has formed on the tree before it reaches diameter d. $h(d)$ is the hazard function relating the TreM formation hazard rate to the diameter of the tree. $h(d)$ is defined as the rate of TreM formation at diameter d conditional on having no TreM until diameter d. Lines (dashed for fir, solid for beech) represent median predictions and gray buffers correspond to 95% predictive intervals.

Figure 2: Observed and predicted proportions of trees having at least one TReM in the data set, for 10-cm tree DBH classes.

For each species and each model, the black dots represent the proportion of trees in a DBH class having at least one TreM. The black lines and grey polygon represent the median and confidence envelope of 1,000 model predictions of TreM formation made by simulating the growth of each tree from a DBH of 5 cm up to its current DBH and the corresponding formation of TreMs. Predictive intervals below vs above the black dots indicate model understimation vs. overestimation of TreM formation for the trees of this DBH class.

Figure 3: Observed and predicted proportion of trees with zero to six TreMs in the data set. For each species and each model, black dots represent the proportion of trees in the data set carying zero to six TreMs. The black lines and grey polygon represents the median and confidence envelope of 1,000 model predictions of TreM formation made by simulating the growth of each tree from a DBH of 5 cm up to its actual DBH and the corresponding formation of TreMs. Predictive intervals below vs above black dots indicate model understimation vs. overestimation of the proportion of trees of a category.
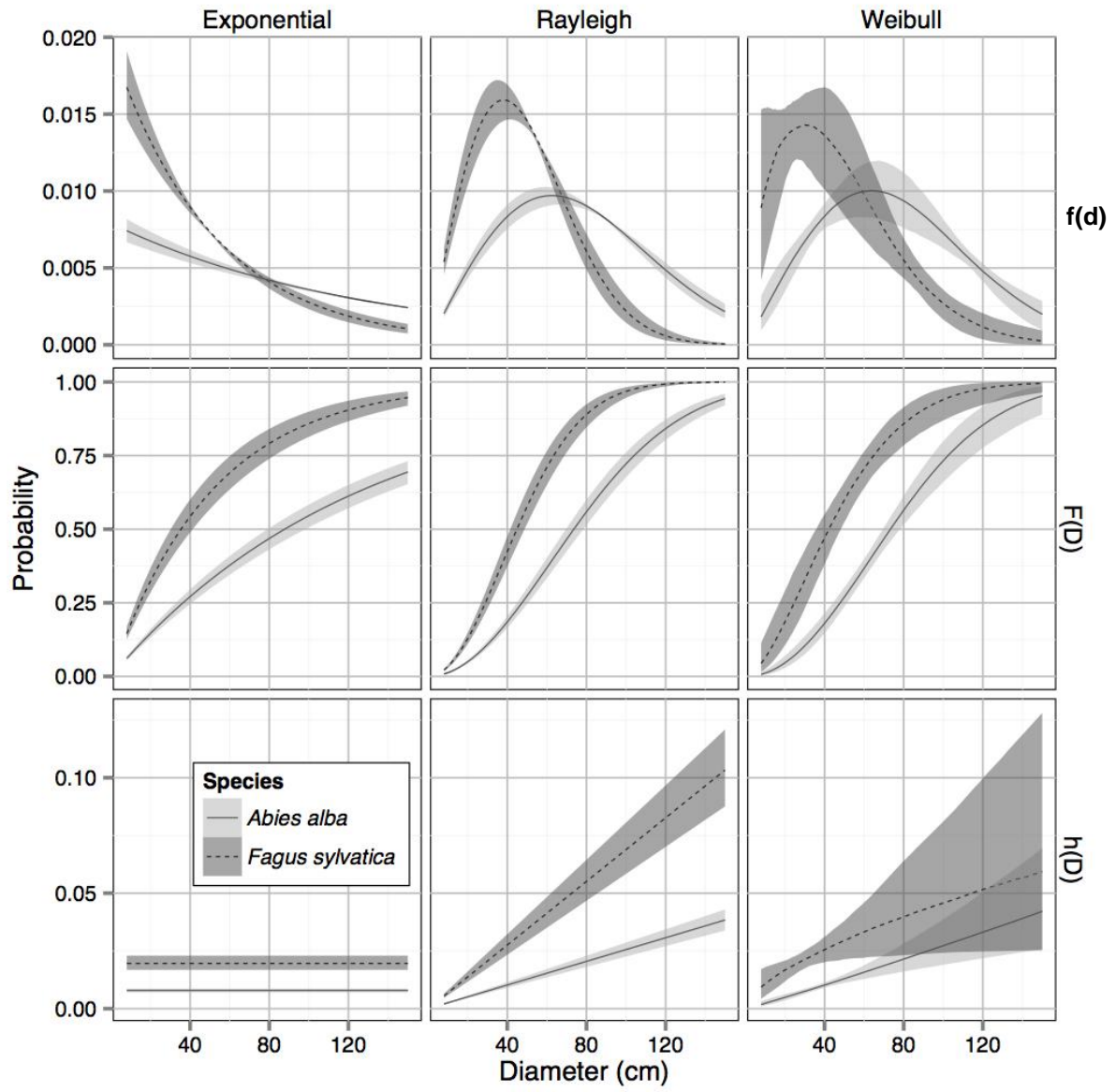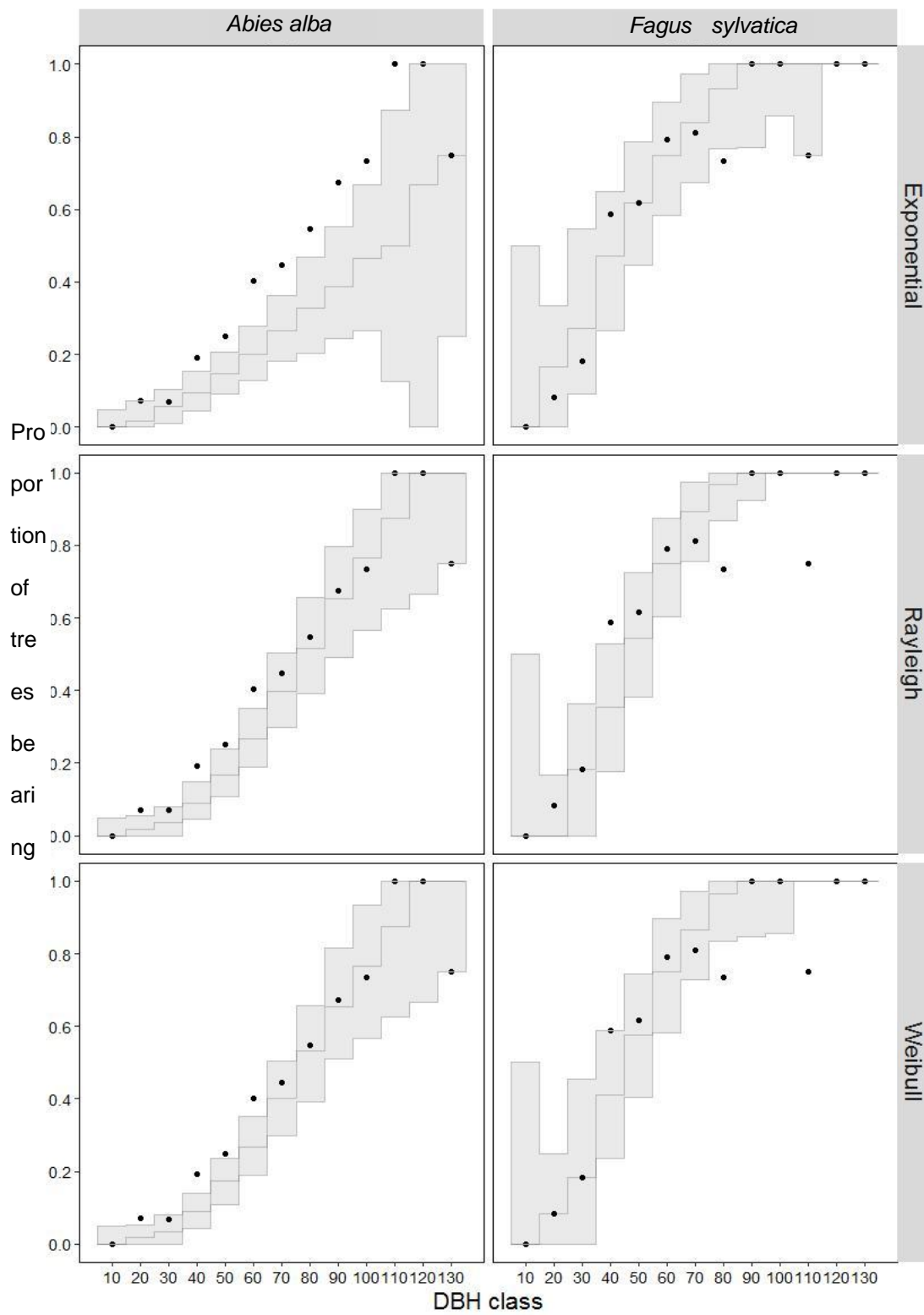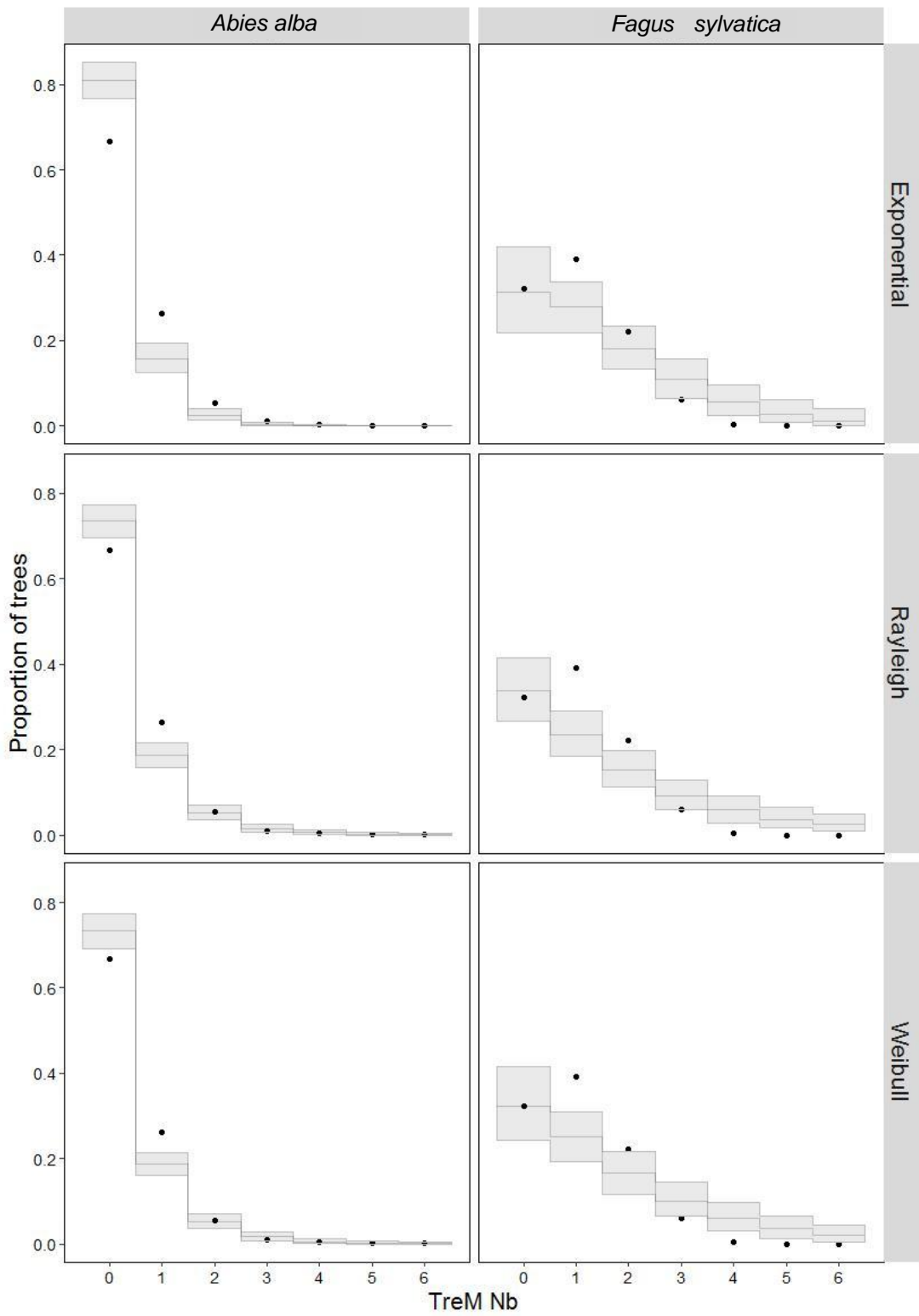
Figure 1

Figure 2

Figure 3