Large-scale informative priors to better predict the local occurrence rate of a rare tree-related microhabitat

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Abstract

Ecological processes associated to rare events are hard to estimate from individual empirical studies. A typical example in forest ecology is the formation of tree-related microhabitats (TreMs) on trees. TreMs are key features for forest biodiversity, and their accumulation rate is a key information to design integrative management strategies. Many types of TreMs are associated to large old trees and show slow ontogenical processes. The rarity of such TreMs (particularly in intensively managed forests) hinder the estimation of their occurrence rate along tree growth. Several meta-analyses accumulated data on TreMs at continental (e.g.

european) scale. However, using data accumulated at these large, heterogeneous scales to orientate management wihtin a specific site remains challenging. Here, we used a large-scale meta-analysis on TreMs occurrence rate along tree growth to build informative priors for a model of basal rot-hole occurrence on oaks within the Grésigne forest, France. We found that calibrating a model without the prior information (i.e. using only Grésigne oak trees) did not reveal any increase of occurrence with tree diameter. Estimation was hindered by confounding effects of plot and tree diameter induced by the local plot-based sampling strategy. Informative priors overcame this confounding effect, restored a positive relationship between diameter and basal rot-hole occurrence but raised the question of whether it introduced biases. A separate validation experiment suggested that it did not. The model with informative priors revealed that the high recruitment of basal rot-holes in Grésigne may be a temporary management effect in stands undergoing conversion from coppice-with-standards to high forest through sprout thinning, which will lead to conservation issues for cavicolous saproxylic species when all conversions are complete. Because using informative priors was simple and beneficial in our study, it should be further explored in other local applied contexts to orientate forest management.

1 Introduction

Some ecological processes are hard to estimate from individual empirical studies. It happens, for instance, when they are associated to rare events, like quantifying the rate of microhabitats formation on trees in the field of forest ecology. Tree-related microhabitats (TreMs) are tree morphological structures that constitute particular and essential substrates for thousands of species [Larrieu et al., 2018]. TreMs thus contribute to forest biodiversity, with heterogeneous effects across forest taxa and across geographical regions [Bouget et al., 2014, Paillet et al., 2018]. Some types of TreMs are inherently rare, because they are caused by rare natural events (e.g lightning scars on trunks). Other types of TreMs have slow ontogenical processes, which make them naturally associated to large, old trees. Short sylvicultural cycles make these types of TreMs rarer and more ephemeral in intensively managed forests than would be expected if unharvested [Vuidot et al., 2011]. The human-induced rarity of TreMs associated to old trees raises conservation issues for associated species, and calls for a better integration of TreMs in a multifunctional approach of forest management e.g. through keeping retention trees in harvested stands [Gustafsson et al., 2012] or extending the rotation length of forest stands [Percel et al., 2018]. Calibrating this type of measures requires quantifying the rate at which target TreMs occur on trees. Unfortunately, TreMs rarity hinders the quantification of their rate of occurrence within a target management site.

Mutualizing the information from many empirical studies is one way out of the difficulty of making inferences from rare events. Meta-analyses follow this rationale [Hobbs and Hilborn, 2006], combining multiple experimental results to synthesize knowledge about some target parameters and their variation among studies. The study of the rate of occurrence of TreMs across forest sites at continental scale by Courbaud et al. [2022] could be classified in this cate-

gory. The authors derived global estimates of occurrence rates for several TreM types, and their analysis revealed a high spatial variance of these rates across sites included in the analysis (see their appendix S6a), in both managed and unmanaged forests. The spatial variance of TreMs occurrence rate could partially stem from the fact that TreM occurrence rate was quantified as a function of tree diameter but overlooked tree age, which is harder to obtain on a large scale basis. Tree diameter being kept constant, many TreM types are known to occur more often on older trees [Kozák et al., 2023]. Therefore any variation in tree growth speed (e.g. due to fertility) can create distortions across sites on the relationship between TreMs occurrence and diameter. In a meta-analysis across France, Germany, Slovakia and Romania, Spînu et al. [2024] could avoid this ambiguity by condidering explicit temporal data, however the time range of their study lead them to focus on the phenomenon of losing ephemeral TreMs in time rather than recruiting TreMs with slow ontogeny. The spatial variance of TreMs occurrence rate can also stem from differences in management that can modulate the rate of occurrence of some TreMs, e.g. those induced by damages during sylvicultural interventions such as bark loss along skidding tracks. More generally, specific processes leading to a TreM can vary a lot among sites (e.g. rockfalls and strong slopes specifically contribute to TreMs creation in mountaneous sites). Overall, the presumably strong variation among forest sites of TreMs occurrence rates questions how global studies like Courbaud et al. [2022] or Spînu et al. [2024] can be used by managers to improve inferences of a TreM occurrence rate within one target forest site.

Bayesian models offer the opportunity to use the information contained in previous studies within a new experiment involving the same processes of interest, under the form of 'informative priors' on associated parameters [McCarthy and Masters, 2005, Clark, 2007]. Informative prior distributions can be ob-

tained from similar empirical studies [Ellison, 2004, Dupuis and Joachim, 2006] or from data generated in pilot experiments [Morris et al., 2013]. They also allow transferring information about target parameters across studies that use different types of data, designs etc. as long as they share parameters that points to the same processes. This has been used to learn from observational data in controlled experiments [McCarthy and Masters, 2005], to bridge gaps in time series of long term monitoring programs [Rodhouse et al., 2019], to generate prior for bird mortality rate based on their bodymass [McCarthy and Masters, 2005], to generate prior for tree mortality based on their growth speed [Morris et al., 2015]. However this has little been applied to the use of large-scale information in specific local case-studies, especially not for the quantification of TreM occurrence dynamics in forest.

Like any regularization procedure [Hooten and Hobbs, 2015], the use of informative priors in Bayesian analyses mechanically improves the precision of estimates (i.e. they decrease the variance of posterior distribution of parameters; McCarthy and Masters [2005], Garrard et al. [2012], Morris et al. [2013]). However, because it comes from other studies, the prior information may be partially unadapted to the current context, and the increase in precision of estimates may come at the cost of larger estimation bias leading to lower predictive accuracy. In their study on tree mortality with informative priors based on tree growth rate, Morris et al. [2015] showed that while the precision of estimates was systematically improved compared to non-informative priors, predictions were improved for only half of the tree species. Beyond the need of building informed priors based on a repeatable and transparent procedure, it is thus necessary to use goodness of fit metrics and validation procedures to assess the potential loss of accuracy [Hooten and Hobbs, 2015, Gelman and Hennig, 2017, Banner et al., 2020].

Here, we aimed at using the information of the continental analysis by Courbaud et al. [2022] on TreMs occurrence rates across Europe and Iran to study the dynamics of one specific TreM type within a single forest, using Bayesian informed priors. We focused on the specific case of basal rot-holes in the Grésigne forest (south-west France). We aimed at illustrating how the precision of estimates about the rate of occurrence of basal rot-holes could be improved in Grésigne by the use of informative prior. We also aimed at quantifying the potential biases and loss of predictive accuracy induced by the use of informative priors. We thus hoped to clarify whether this technically simple procedure can generate better local information on TreMs, hence opening the way to designing well-adjusted multifunctional forest management strategies.

2 Material and methods

2.1 Oaks and basal rot-holes data in Grésigne

We focused on one TreM type, basal rot-holes, which corresponds to the category 'trunk base rot-hole' in the typology of Larrieu et al. [2018]. Basal rot-holes harbour a chamber that is closed on top and completely protected from surrounding microclimate and rain. They contain wood mould, the quantity of which increases with the development stage of the hole. The bottom of the hole is in contact with the ground although the hole entrance can be higher on the trunk.

We surveyed basal rot-holes in the Grésigne forest, a State forest of south-west France, in the Tarn department. It is a lowland forest, covering c.a. 3500 ha, and dominated by sessile oak (*Quercus petraea*). The forest has undergone a gradual shift of management from coppice-with-standards to high forest, initiated in late XIXth century. As a result, stands are currently managed in a

heterogenous way: oldest stands (more than 120 years since last cut) are still under conversion, and are thus managed as high forest by singling (sprout thinning); youngest stands (less than 120 years since last cut) has ended conversion, and are managed as classic high forest. The conversion from coppice-with-standards to high forest through singling has contributed to generate a high occurrence of rot-holes at the bottom of oak trunks, particularly large holes at advanced development stage (*sensu* Larrieu et al. [2018]). As a result, the Grésigne forest harbours an outstanding biodiversity associated to such basal rot-holes, including the violet click beetle *Limoniscus violaceus* which is listed in the second annex of the Habitat Directive [Gouix et al., 2015].

Nine 1-ha circular plots (i.e. radius of 57 m) were surveyed in 2021, six being located within stands that are still under conversion, and three within stands where conversion was complete and a new sylvicultural cycle of high forest has been initiated (Figure 1). These plots were part of the BloBiForM project, which aimed at generating a fractal sampling design [Laroche, 2022] to study β-diversity among ecological communities inhabiting basal rot-hole over a range of spatial scales from tree to forest. All the trees within plots were inspected by two operators. For trees with diameter at breast height (DBH) above 17.5 cm, operators noted the tree species, the tree DBH and whether the tree harboured a basal rot-hole. The data obtained during this first campaign was used to calibrate the local model of basal rot-hole occurrence below.

Seven additional plots were surveyed in 2022 (Figure 1). Four plots were located in stands under conversion, one in a stand where conversion was complete. The two remaining plots were overlapping the two types of stands, but one was predominantly located in a stand undergoing conversion ($BLO16$) while the other was predominantly in a stand where conversion was complete ($BLO22$). Tree sampling occurred according to the same protocol (circular plots, two oper-

ators, DBH above 17.5 cm etc.). This new data was used as a validation dataset below. Although a fraction of the Grésigne forest (c.a. 40 ha) is a protected left-aside area, the $9 + 7 = 16$ sampled plots of our study were all located in managed stands.

2.2 Continental model of basal rot-hole occurrence

Courbaud et al. [2017] suggested to model the occurrence of TreMs on trees in forest using the framework of survival analysis, which relies on defining a survival function $S(d)$ corresponding to the probability that a tree has not developped a TreM of a given type yet when reaching a DBH d (expressed in cm). They used a Weibull distribution to model survival functions:

$$S(d) = e^{-\left(\frac{d}{\lambda}\right)^k} \tag{1}$$

where $\lambda > 0$ is a scaling parameter on tree DBH (i.e. λ is the tree DBH at which the probability of having developped a TreM of target type becomes higher than $1 - \exp(-1) \approx 63\%$), while parameter $k > 0$ drives the shape of the probability increases. If $k > 1$, the rate of TreM formation on non-bearing trees increases with the DBH. Conversely, if $k < 1$, the rate decreases with the DBH. Courbaud et al. [2022] conducted a Bayesian estimation the survival function parameters for 11 types of TreMs based on the observation of 80,099 living trees from 19 species groups in plots spread across 307 forests of Europe and Iran [Courbaud et al., 2021]. The authors built a separate model for each TreM type, where the scale parameter $\lambda = \lambda_{jms}$ depended on tree species j, management regime m ('managed' versus 'unmanaged') and forest site identity s (plot identity within forest site was not included in the analysis):

$$\log\left(\lambda_{jms}\right) = \alpha_j + \beta \times 1_{m=\text{'managed'}} + \Delta_s \tag{2}$$

The forest site effect Δ_s was modeled as a random effect following a centered normal distribution with variance σ_s^2. The shape parameter $k = k_j$ depended on tree species only. The log parameter $\theta_j = \log(k_j)$ was used in the estimation.

The grain of TreM typology used by Courbaud et al. [2022] was coarser than our goal here: all types of rot holes containing wood mould were grouped together in a single category including 'Trunk base rot hole', the type of interest here), but also 'Trunk rot hole', 'Semi-open trunk rot hole', 'Chimney trunk base rot hole', 'Chimney trunk rot hole' (see Larrieu et al. [2018] for a description of these items). We therefore re-used their code and model to generate sampled posterior distribution of parameters α_{oak}, β, θ_{oak} and σ_s^2 for basal rot-holes only. We only considered the 'Quercus' species group, which reduced the dataset to 8684 trees in 146 forests. We used a MCMC approach through a Gibbs sampling algorithm provided by the package *rjags* [Denwood, 2016]. For each estimation, we implemented four Markov chains with independent initialization. We applied a 5×10^3 steps burning period, followed by 7×10^3 steps where parameter values were recorded every 15 steps, resulting in 500 samples in each chain. We assessed the quality of the convergence of the Markov Chains by checking whether the Potential Scale Reduction Factor index (PSRF) was less than 1.1 for all parameters and that the Monte Carlo standard errors were less than 5% of the standard deviation of the parameters [Denwood, 2016].

We recorded the sampled posterior distribution of the four parameters: α_{oak}, β, θ_{oak} and σ_s.

2.3 Local model of basal rot-hole occurrence in Grésigne

The process of basal rot-hole occurrence on oaks in Grésigne was also modeled through a Weibull survival function based on tree DBH. We assumed that the scale parameter of survival function λ_{ip} for tree i in sampled plot p could be

expressed as:

$$\log(\lambda_{ip}) = \alpha_{\text{oak}} + \beta + \Delta_{\text{Grésigne}} + \zeta c_{ip} + E_p \tag{3}$$

where: $\Delta_{\text{Grésigne}}$ is a random Grésigne site effect, following a centered normal distribution with variance σ_s^2 ; α_{oak}, β and σ_s^2 are parameters of the continental model ; the plot effect E_p was modeled as a random effect following a centered normal distribution with variance σ_p^2. We defined a 'conversion' covariate c_{ip}, equal to 1 if the conversion towards high forest was still in progress for the stand where tree i of plot p lies (and current treatment is thus high forest by singling), and to 0 if the conversion was over. In general, all the trees within a plot belonged to the same stand, and thus had the same value of c_{ip}. The effect of being in a stand under ongoing conversion is denoted ζ. The shape parameter k was constant for all trees. When performing estimation, we considered $\alpha_{\text{oak}} + \beta + \Delta_{\text{Grésigne}}$ as a single 'intercept' parameter, denoted α. We also considered the parameter $\log(k) = \theta$ rather than k itself. Using a Bayesian framework for the estimation required to define priors for the three parameters α, θ and σ_p. We considered two alternative strategies.

Non-informative priors — We assumed that the prior distribution of parameters α and θ were independent, normal distributions with mean 0 and variance 10^4. The prior distribution on parameter ζ was defined to ensure that α and $\alpha + \zeta$ had identical and independent prior distributions. In practice, this led us to use a normal prior distribution for ζ, with mean 0 and variance 2×10^4, while setting the covariance between ζ and α at -10^4. The prior on σ_p was set as a uniform distribution between 0 and 200.

Informative priors — We defined a prior distribution for $\Delta_{\text{Grésigne}}$ as a normal distribution with mean 0 and variance equal to the mean of sampled

posterior distribution of σ_s^2 in the continental model. The covariance between $\Delta_{\text{Grésigne}}$ and other parameters prior distributions was set to 0. Recalling that the intercept of the local model α equals $\alpha_{\text{oak}} + \beta + \Delta_{\text{Grésigne}}$, we generated a prior distribution for α by combining the posterior multivariate normal distribution of $(\alpha_{\text{oak}}, \beta)$ derived from the continental model (see section 2.2) with our assumptions on $\Delta_{\text{Grésigne}}$ prior. We directly used the posterior normal distribution of θ_{oak} derived from the continental model of section 2.2 as a prior for θ in the local model. The prior distribution on parameter ζ was defined to ensure that α and $\alpha + \zeta$ had identical and independent prior distributions. In practice, this led us to use a normal prior distribution for ζ, with mean 0 and variance $2 \times V(\alpha)$, where $V(\alpha)$ is the variance of the informative prior set on α, while setting the covariance between ζ and α at $-V(\alpha)$. The parameter σ_p followed a uniform distribution between 0 and 200, independent from other parameters prior distribution.

We derived a sampled posterior distribution of parameters α, θ, σ_p in either case using a MCMC approach. We used a Gibbs sampling algorithm provided by the package *rjags* [Denwood, 2016], on the *R* software platform (v4.3.3; R Core Team [2023]). For each estimation, we implemented four Markov chains with independent initialization. We applied a 10^5 steps burning period, followed by 2×10^6 steps where parameter values were recorded every 2.5×10^3 steps, resulting in 800 samples in each chain. We checked for pseudo-replication in the sampled posterior distribution using Markov chains autocorrelation diagrams, and chains were trimmed when necessary. We checked for stationarity using visual inspection of chains and Gelman statistics. Codes and diagnostics are provided in a public repository online [Cottais and Laroche, 2024].

2.4 Goodness-of-fit of models

We first assessed the goodness of fit of each calibrated model through a bootstrap procedure. For each parameter value in the trimmed sampled posterior distribution, we simulated the presence-absence of basal rot-holes on all trees of the calibration dataset. We recorded three types of statistics: the number of basal rot-holes in each stand, the total number of basal rot-holes on oaks with DBH below 35 cm (median DBH of the dataset) and the total number of cavities on oaks with DBH above 35 cm. We assessed whether the values of statistics in the real dataset was comprised within a likely range of simulated values. To do so, we computed a bilateral p-value based on the empirical quantile of the observed value within simulated values (for number of cavities per plot) or resorted to simple visual inspection (for the two other statistics).

We compared the goodness of fit of calibrated models using the Deviance Information Criterion (DIC; Spiegelhalter et al. [2002], McCarthy and Masters [2005]), which accounts for the fact that using informative priors decreases the effective number of degrees of freedom used by the model. The DIC is computed as $2 \times \bar{D}(\mathbf{\Theta}) - D(\bar{\mathbf{\Theta}})$, where $\bar{D}(\mathbf{\Theta})$ is the mean deviance computed across the posterior distribution of parameters $\mathbf{\Theta}$ and $D(\bar{\mathbf{\Theta}})$ is the deviance at the mean posterior estimates of parameters. Means are computed empirically from the sampled posterior distributions. To compute DIC indices, we used $\mathbf{\Theta} = (\log(\alpha), \theta, E_1, ..., E_9)$. A lower DIC by more than two points is classically considered as a signal of significantly better fit.

2.5 Predictive performance of models

We used the 2022 validation dataset to assess the predictive performance of the two models calibrated in previous sections. For each model and each parameter value in the trimmed sampled posterior distribution, we computed the predicted

probabilities of presence of basal rot-holes in all the trees of the validation dataset. The plot effect (E_p in eq. (3)) was set to 0. In the two plots overlapping stands with distinct conversion statuses ($BLO\,16$ and $BLO\,22$), because the exact position of trees within the plot had not been recorded in the validation dataset, we attributed the conversion status of the stand with the highest overlap to all trees of the plot. For each set of predicted probabilities, we computed two metrics: the root mean squared error (RMSE) of prediction between predicted probability and observed basal rot-hole presence-absence across all the trees of the dataset and the deviance of the model on the validation dataset, defined as $-2\log(\mathcal{L})$ where $\mathcal{L}$ is the likelihood of the model upon validation data. We thus obtained sampled posterior distributions of RMSE and deviance for the two models.

3 Results

3.1 Sampling effort

Operator pairs were able to survey 2 plots per day of fieldwork on average. The overall study thus took c.a. 17 operator.days. In 2021, 1462 oak trees were described over the nine surveyed plots. In 2022, 971 oak trees were described over the seven surveyed plots. The data has been made available on a public repository [Laroche, 2024]. In the 2021 calibration dataset, oaks of plots $BLO\,12$ and $BLO\,17$ harboured markedly lower DBH values than those of other plots, which was expected, given that they were the only plots of the 2021 survey where a cut occurred less than 60 years ago (Figure 1). Globally there seemed to be a positive relationship between oak trees DBH and their propensity to harbour a basal rot-hole (Figure 2B).

The MCMC algorithm used to sample the posterior distributions of parame-

ters yielded 460 exploitable samples in 91 minutes for the non-informative priors and 3200 exploitable samples in 40 min for the informative priors. An estimation summary is provided in Table 1.

3.2 Model fit with non-informative priors

The occurrence model of basal rot-holes calibrated on the 2021 dataset with non-informative priors yielded a correct fit of the number of cavities in each plot, the number of cavities on large (DBH above 35 cm) and small (DBH below 35 cm) oaks (Fig. S1). The DIC of the model was 750.7.

The posterior distributions of parameters α and ζ were highly variable, spanning more than a hundred of magnitude orders of the scaling parameter λ (Tab. 1). The joint posterior distribution of α and θ was widely spread along a line of low identifiability (Fig. 3). The same phenomenon occured between $\alpha+\zeta$ and θ. These lines indicated an absence of effect of oak DBH on the occurrence of basal rot-holes: the model did not detect any increase of the occurrence probability of a basal rot-hole on larger oak trees. The predicted probability of occurrence of a basal rot-hole as diameter increases was nearly flat, irrespective of conversion status (Fig. 4A), as if a random fraction of oak trees carried a basal rot-hole before reaching a DBH of 17.5 cm, and no holes appeared later on.

Despite the high variability of the posterior distribution of the conversion effect ζ, its posterior 95% credibility interval did not include 0 and comprised only strictly negative values (Tab. 1), which indicated higher occurrence probability of basal rot-holes in stands still undergoing conversion (c.a. 15% of oak trees; Fig. 4A) compared to stands where conversion was complete (c.a. 2% of oak trees; Fig. 4A).

3.3 Model fit with informative priors

The occurrence model of basal rot-holes calibrated with the informative priors on the 2021 survey yielded a correct fit of the number of cavities in each plot, the number of cavities on large (DBH above 35 cm) and small (DBH below 35 cm) oaks (Fig. S2). The DIC of the model with informed priors was 751.2. Therefore, the use of informed priors did not induce a significant increase in DIC compared to non-informative priors, suggesting an equal quality of fit between the two calibrated models.

As expected, using the informative priors improved the precision of the posterior sampled distribution of parameters compared to the model with uninformed priors (Tab. 1; Fig. 3). Quantitatively, the variance on θ (resp. α) posterior distribution between models with non-informative and informative priors was reduced by a factor of c.a. 46 (resp. 58).

The posterior distribution of θ was similar to the corresponding informed prior distribution (Tab. 1). The posterior distribution of α (stands where conversion is complete) was located around the same values as the corresponding informed prior distribution (Fig. 3; Tab. 1), but was more narrow. By contrast, the posterior distribution of $\alpha + \zeta$ (stands where conversion is still ongoing), clearly departed from the informative prior distribution, being markely shifted towards lower values (Fig. 3), which suggested that rot-holes tended to occur earlier with tree growth in Grésigne stands under conversion than expected from the prior.

Posterior distributions of parameters suggested that oak tree diameter had an effect on the occurrence of basal rot-holes (Fig. 4B). The 95% θ parameter contained only negative values, suggesting that the rate of basal rot-hole creation on non-bearing oak trees increased with DBH: large non-bearing trees tended to develop basal rot-holes faster per DBH growth unit than smaller trees. The 95%

credibility interval of the conversion effect ζ did not overlap 0, and only included negative values. This indicated that basal rot-holes tend to occur faster with DBH increase in plots that are still under conversion, compared to plots where conversion is complete (Fig. 4B).

3.4 Comparing predictive abilities of models

Both models calibrated with non-informative and informative priors showed better prediction performance on the 2022 validation dataset than a null model randomizing basal rot-holes among trees (Figure 5). The model calibrated with informative priors showed better prediction performance than the model calibrated with non-informative priors both in terms of RMSE and deviance.

4 Discussion

In our study, we aimed at exploring whether the use of informative priors obtained from a continental study could contribute to a better estimation of basal rot-holes occurrence rate on oaks of the Grésigne forest than using local data alone. We found that calibrating the model of basal rot-holes occurrence rate without prior information did not reveal any effect of DBH on rot-hole occurrence. Accurate estimation was hindered by confounding plot and DBH effects induced by the plot-based sampling strategy. Informative priors contributed to overcome this confounding effects of DBH and plot, yielded a positive relationship between DBH and basal rot-holes occurrence in line with previous results. However, this raised the question of whether these priors introduced biases. Our analyses of fit and our validation experiment tended to show that they did not. The model with informative priors contributed to reveal that the high recruitment of basal rot-holes in Grésigne may be a temporary management effect in stands undergoing conversion from coppice-with-standards to

high forest through sprout thinning, which will lead to conservation issues for cavicolous saproxylic species when all conversions are complete. Because using informative priors was simple and beneficial in our study, we advocate that it should be further explored in local applied contexts. Below, we further discussed each of these points in turn.

Calibrating the model of basal rot-holes occurrence rate without prior information did not reveal any effect of DBH — A basal rot-hole can show various development stages, but it is likely to last as long as the bearing tree persists [Larrieu et al., 2022], contrary to other TreMs that can disappear or evolve to new types [Spînu et al., 2024]. Therefore, the probability of observing a basal rot-hole on a tree must increase in time. Because the DBH of a tree also increases in time, one expects a positive correlation between DBH and basal rot-hole occurrence. The absence of relationship between DBH and basal rot-hole occurrence in the model calibrated with non-informative priors was therefore surprising and at variance with previous studies [Courbaud et al., 2017, 2022, Kozák et al., 2023]. Our result suggested that tree holes would not develop slowly with tree growth, but rather appear on a random fraction of trees before they reach the 17.5 cm DBH threshold at which our observations started. This scenario was not completely unrealistic in Grésigne though, because many stands are still undergoing conversion from coppice-with-standards to high forest by singling. In high forest generated from sprout thinning, the tree stump, where the basal rot-holes may occur, can be older and larger than the stem which is measured. Gouix et al. [2015] illustrated an effect of this historical process in Grésigne forest by showing that the diameter at 30 cm height from the ground explained better the presence of the violet click beetle (*L. violaceus*) in basal rot holes than DBH of stems. However this conversion effect did not explain the absence of relationship between DBH and basal rot-hole occurrence

in stands where conversion was complete (managed as regular high forest). On that respect, it should be noted that the management history of the Grésigne forest lead to a situation where stands undergoing conversion are more advanced in their sylvicultural cycle than plots where conversion is complete. As a result, plots where the conversion was complete tended to harbour oak trees with a lower and narrower range of DBH, which rendered the estimation of an apparition process of basal rot holes along tree growth difficult. We may therefore interpret the output of the model with non-informative priors as the product of: (i) an absence of clear basal rot-holes accumulation process with DBH in stands undergoing conversion, because of the partial decoupling between stump and stem ages; (ii) a lack of statistical power in stands where conversion is complete because of low mean and low variance variance in DBH values.

The plot-based sampling strategy structurally lead to confounding plot and DBH effects that hindered estimation. — Finding no effect of DBH on basal rot-hole occurrence in the model with non-informative priors contrasted with the pattern observed in the 2021 dataset, where the proportion of oak trees with a basal rot-hole clearly increased with DBH. This contrast came from the confounding effect between plot conversion history (ongoing versus complete) and the average tree diameter in the plot: once conversion history is accounted for, there is too little variation in DBH within the subsequent categories to detect an effect of DBH. This difficulty is more general than the particular case of Grésigne. Were it not the specific conversion history of the forest, one would still expect a confounding effect between plot and DBH effects to arise in a managed forest harbouring mostly even-aged, high forest treatments in stands, as trees from the same plot tend to harbour similar DBH values. This problem has been little investigated in previous studies on TreMs dynamics [Courbaud et al., 2017, 2022, Spînu et al., 2024] where plot effects

were not included except through undirect covariate (e.g. altitude). One way of overcoming this confounding effect could be to drop the plot-based sampling strategy and e.g. sample individual trees across the whole forest instead, but it would considerably increase the time spent per tree, as distances needed to go to the next tree become larger when trees are not aggregated in space [Laroche, 2022].

Informative priors contributed to overcome the confounding effects of DBH and plot. — Introducing informative priors removed the pseudo-identifiability constraint induced by the confounding effect between DBH and conversion effect by forcing shape and scale parameters of the occurrence rate function to lie in a narrow area of the parameter space. This forcing restored the positive relationship between basal rot-hole occurrence and diameter expected from a temporal process of appearance. However, given its strong impact on the analyses, one must question whether the informative prior used is relevant to the particular context of Grésigne. Having adopted, a transparent, reproducible methodology to obtain these priors is an essential pre-requisite to discuss this point [Dennis, 1996, McCarthy and Masters, 2005]. This allows raising two potential issues in our case. First, informative priors are obtained from a study where no plot effect was included [Courbaud et al., 2022], which amounted to remove the plot-DBH confounding effect within high forest sites by arbitrarily attributing all the effect to DBH. Generating our priors from this study may have implicitly propagated this convention to our results. Second, a fraction of plots in Grésigne are managed in a quite specific way compared to traditional high-forest (the conversion dynamics through sprout thinning), and management is known to be a strong driver of TreMs dynamics [Vuidot et al., 2011]. The international network of forest sites used to build the informative prior may therefore be little representative of Grésigne forest, potentially generating biased

estimates, as it could be observed in other empirical studies [Morris et al., 2015].

A careful use of informative priors did not generate estimation biases and increased the predictive power. — We could bring several elements to support the idea that informative priors did not generate biased estimates. Our analyses of fit (DIC) and predictive accuracy (validation on new data) concurred to indicate that, in our study, the use of prior information improved the predictive perfomance of the model without degrading the fit. The *a priori* DBH effect generated by informative priors thus proved to be a worthy addition to the local analysis of Grésigne basal cavities. Our choice of informative priors proved successful because our local model also allowed for differences in basal rot-holes occurrence rate between stands undergoing conversion and stands where conversion was complete. Thanks to this decoupling, the data acquired in stands under conversion could generate a shift between the informative prior and the posterior distribution of basal rot-holes occurrence rate whereas the data from stands managed as classic high forest did not alter the informative prior. Recalling that informative priors are built from a large number of managed oak forest at continental scale by Courbaud et al. [2022], our results thus suggested that stands undergoing conversion in Grésigne are atypical in terms of basal rot-holes occurrence with respect to other contexts encountered at continental scale, as stressed by the monography of Ducasse and Brustel [2008]. By contrast, stands where conversion is complete harboured more classic rot-holes occurrence rates, within the range of what can be observed at continental scale. Whether the use of large-scale informative priors to study TreMs dynamics can be generalized to other forests and TreMs without bias is an open question. In a study on tree mortality, Morris et al. [2015] showed that the same procedure could generate bias in some contexts and no bias in others, which invites us to remain cautious. A more systematic exploration of this feature, e.g. through leave-one-

out strategies on sites of large-scale TreMs datasets like Courbaud et al. [2021] would provide a more general view on that respect. However, we warn against using informative priors on TreMs dynamics in a standardized and systematic way without careful case-by-case adaptations: the success of our approach here is partly due to the fact that we combined large-scale prior information with a specific, local knowledge of the forest heterogeneous management which was implemented as a conversion effect into the model. The key of success probably lies in analyzing the specifities of the local context with respect to the cases that were used in previous studies to decide whether and how to use informative priors.

The high recruitment of basal rot-holes in Grésigne is a temporary management effect. — The conversion from coppice-with-standards to high forest strongly increased the presence of basal rot-holes within plots of Grésigne. This effect was sufficiently strong to be detected even with non-informative priors. The use of informative priors further lead to detect that basal rot-holes occured earlier with oak tree growth in stands under conversion. While sprout thinning is the major driver of basal rot-hole formation in the former situation, only weaker factors remain active in classic high forest, mostly damages related to logging and skidding. These findings raised a conservation issue. Since classic high forest treatment is not generating basal rot-holes at the same rate as the conversion phase, the basal rot-holes renewal will necessarily decrease as more stands end their conversion, and the Grésigne forest may not remain a hotspot of basal rot-holes in the long term. Also, basal rot-holes generated by logging damages on trees may be of smaller size (a critical feature for saproxylic beetles; Gouix et al. [2015]) and lower quality than holes induced by sprout thinning in terms of habitat for rot-hole dwelling species. We did not explore this qualitative dimension in our study, although more elaborated models of basal rot-holes

development stages [Larrieu et al., 2018] with tree growth could be developped in this direction. A reasonable integrative management action in line with our results would thus be to keep oak trees starting back from natural sprouting disseminated within the new stands, to ensure the recruitment and the connectivity of future basal rot-holes, as suggested by Gouix [2011]. Our conclusions will nonetheless need reevaluation in the future, for climate-driven changes in growth regime and mortality may affect the relationship between diameter and basal rot-hole presence. This is likely to happen in our context, since sessile oaks in Grésigne forest are at the edge of their environmental niche and face low-fertility conditions that make them vulnerable to climate changes.

Using informative priors was simple and beneficial in our study, and should thus be further explored in local applied contexts. — With 17 operator.days of fieldwork (the effort needed to collect the 2021 calibration dataset) and less than one hour of computing on a conventional laptop, we have been able to derive a model of basal rot-hole occurrences combining local data and informative priors which proved able to (i) reveal challenges to come for maintaining the availability of basal rot-holes in Grésigne and (ii) yielded better estimation and prediction than a model based on local data only. Such model could now be coupled with management scenarios (e.g. in forest simulation platforms; Dufour-Kowalski et al. [2012], Courbaud et al. [2015]) in order to design viability pathways for basal rot-holes and associated biodiversity as the renewal of the forest goes on. Our approach based on coupling regional priors with a local, small calibration dataset is light-to-implement and very general, and we strongly encourage forest researchers and local managers to apply and test it in their contexts, for the assessment the TreM dynamics and beyond.

Acknowledgements

FL thanks Y. Grzelec, the head of Grésigne forest management unit for his help in planning the fieldwork, A. Ardanuy-Gabarra, A. Brin, W. Heintz, S. Ladet, J. Molina and G. Parmain for their help during the field work.

This work was supported by the ANR JCJC BloBiForM project (grant ANR-19-CE32-0002-01). A CC-BY public copyright license has been applied by the authors to the present document and will be applied to all subsequent versions up to the Author Accepted Manuscript arising from this submission, in accordance with the grant's open access conditions.

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Tables and figures

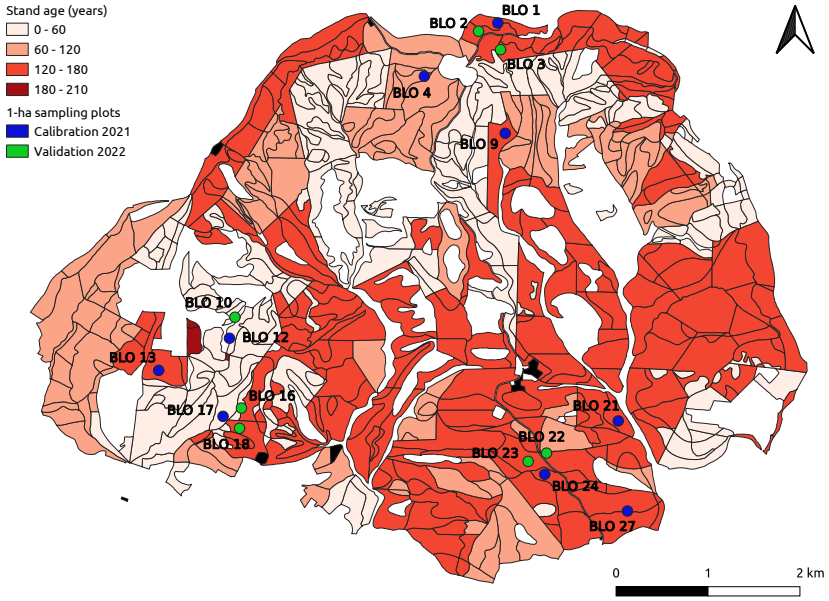

Figure 1: Study sampling design within the Grésigne forest.

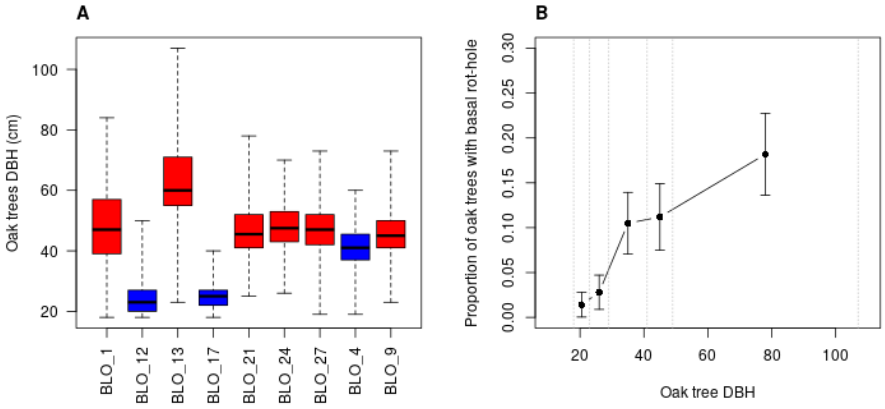

Figure 2: Summary of oak trees DBH and basal rot-hole presence observed during the 2021 survey Grésigne. Panel A: distribution of oak trees DBH within each plot, boxes show extreme values, quartiles and median. Red boxes correspong to plots undergoing conversion, blue boxes correspond to plors where conversion was complete. Panel B: proportion of oak tree bearing a basal rot-hole in five DBH categories. Categories were delineated using quantiles 0.2, 0.4, 0.6 and 0.8 of the DBH distribution. Borders of the bins are shown with vertical dotted grey lines. The proportion of trees bearing a basal rot-hole is indicated in each bin using a dot. Bars indicate an asymptotic 95% confidence interval of the proportion.

Parameter	Without information					With information				
	Prior		Posterior			Prior		Posterior		
	mean	std. dev.	mean	std. dev.	95% CI	mean	std. dev.	mean	std. dev.	95% CI
α	0	100	139	63	$[38, 280]$	7.61	1.47	7.98	0.54	$[7.03, 9.09]$
θ	0	100	-3.45	0.54	$[-4.29, -2.21]$	-0.133	0.077	-0.161	0.080	$[-0.318, -0.007]$
σ_p	100	57.7	17.1	14.3	$[1.7, 51.0]$	100	57.7	0.41	0.25	$[0.05, 1.01]$
ζ	0	141	-74.5	38.0	$[-163.7, -14.9]$	0	2.08	-2.04	0.49	$[-3.063, -1.13]$
E_1	-	-	-12.0	12.1	$[-40.8, 4.6]$	-	-	-0.41	0.31	$[-1.08, 0.07]$
E_{12}	-	-	4.5	17.8	$[-19.3, 42.9]$	-	-	-0.03	0.37	$[-0.79, 0.75]$
E_{13}	-	-	-7.1	11.8	$[-35.5, 12.6]$	-	-	-0.13	0.30	$[-0.79, 0.40]$
E_{17}	-	-	17.1	24.9	$[-7.8, 71.6]$	-	-	0.28	0.41	$[-0.35, 1.29]$
E_{21}	-	-	2.7	10.5	$[-16.8, 24.6]$	-	-	0.02	0.28	$[-0.56, 0.58]$
E_{24}	-	-	-0.7	11.0	$[-23.4, 25.7]$	-	-	-0.06	0.29	$[-0.71, 0.51]$
E_{27}	-	-	7.8	12.2	$[-11.2, 39.9]$	-	-	0.16	0.29	$[-0.37, 0.80]$
E_4	-	-	-12.7	17.8	$[-54.4, 12.7]$	-	-	-0.27	0.42	$[-1.24, 0.42]$
E_9	-	-	11.1	13.0	$[-7.7, 42.6]$	-	-	0.24	0.28	$[-0.27, 0.85]$

Table 1: Summary of estimation of model of basal rot-hole occurrence. Pearson correlation between α and θ informative prior distributions equaled -0.18. Pearson correlation between α and ζ informative prior distributions equaled $-1/\sqrt{2} \approx -0.7$.

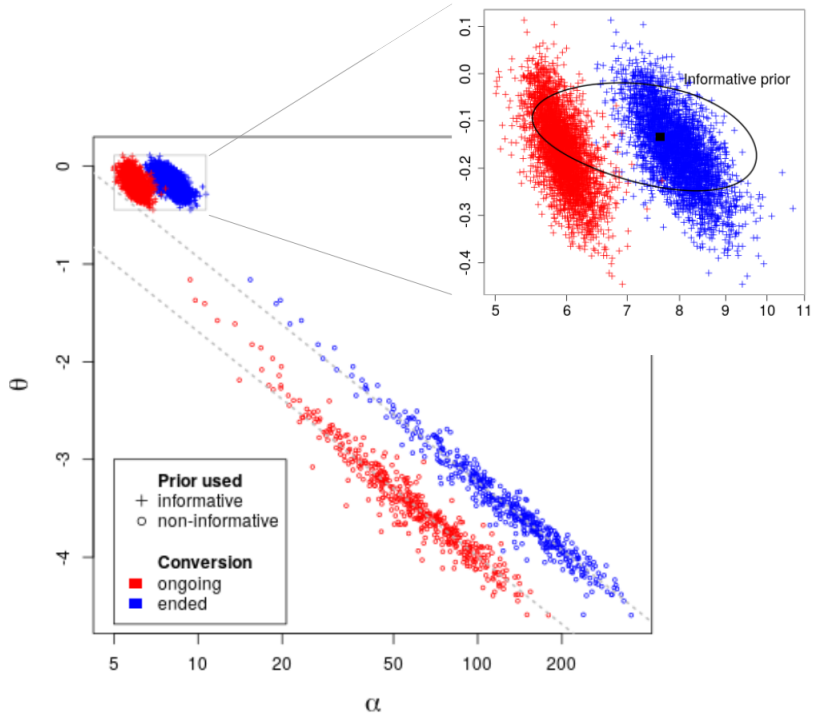

Figure 3: Sampled posterior distribution of the occurrence model parameters α (in blue), $\alpha + \zeta$ (in red) and θ for basal rot-holes of Grésigne, calibrated on 2021 survey, with non informative (cicles) or informative (crosses) priors. The grey dashed lines show couple of parameters that yield to the same prediction of uniform probability across trees for large absolute parameter values. The area around the sampled posterior distribution with informative priors is zoomed, and the informed priors distribution is presented in black (square: mean of informative prior distribution; ellipse: one standard deviation to the mean).

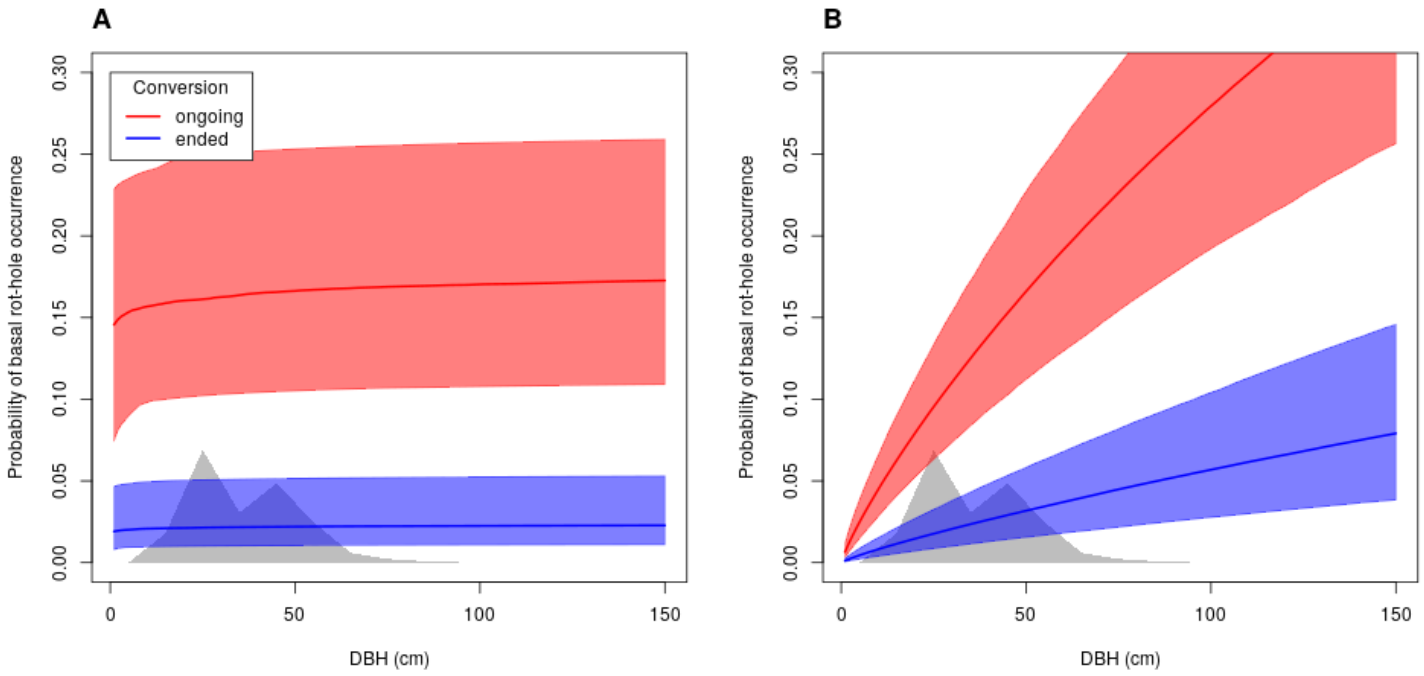

Figure 4: Probability of occurrence of a basal rot-hole on Grésigne oaks as diameter increases, calibrated on the 2021 survey with non-informative (panel A) and informative (panel B) priors on parameters. Red indicates probability in plots undergoing conversion, blue indicates probabilities in plots that have ended conversion. The grey profile in the background recalls the distribution of oak DBH in the dataset.

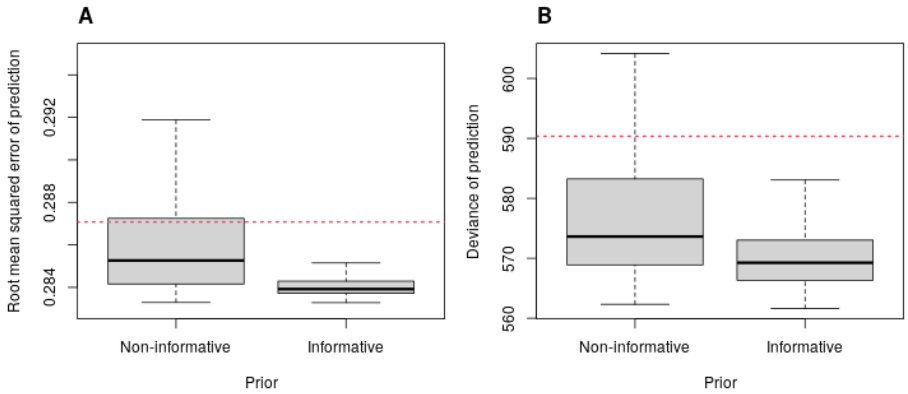

Figure 5: Prediction error of models with non-informative and informative priors on the 2022 validation dataset. Prediction error is quantified as root mean squared error of prediction (RMSE) on basal rot-hole presence on trees (Panel A) or the deviance of models on the validation dataset (Panel B). In both panels, the red horizontal dashed line presents the predictive performance of a null model based on the proportion of basal rot-hole in the validation dataset, as a benchmark.

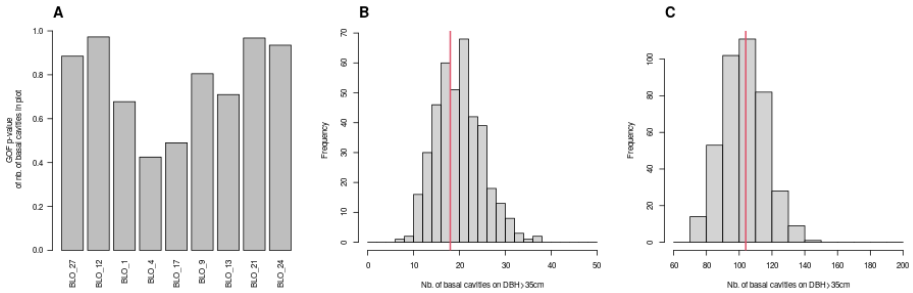

Fig. S1: Goodness-of-fit (GOF) of the occurrence model for basal rot-holes of Grésigne with non-informative priors, calibrated on 2021 survey. Panel A: GOF p-value of a bilateral test for the number of basal rot-holes in each plot. Panel B and C: simulated (grey histogram) versus observed (red bar) number of basal rot-holes on trees with DBH below 35 cm (panel B) and above 35 cm (panel C) over the 2021 survey.

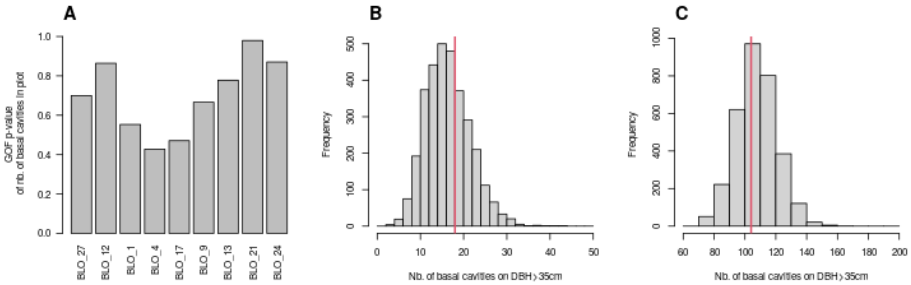

Fig. S2: Goodness-of-fit (GOF) of the occurrence model for basal rot-holes of Grésigne with informed priors calibrated on 2021 survey. Panel A: GOF p-value of a bilateral test for the number of basal rot-holes in each plot. Panel B and C: simulated (grey histogram) versus observed (red bar) number of basal rot-holes on trees with DBH below 35 cm (panel B) and above 35 cm (panel C) over the 2021 survey.