Forest Ecology and Management 487 (2021) 119023

Contents lists available at ScienceDirect

Forest Ecology and Management

journal homepage: www.elsevier.com/locate/foreco

Choosy beetles: How host trees and southern boreal forest naturalness may determine dead wood beetle communities

Ryan C. Burner [a,*], Tone Birkemoe [a], Jörg G. Stephan [b], Lukas Drag [c], Jörg Muller [c,d], Otso Ovaskainen [e], Mária Potterf [f], Olav Skarpaas [g], Tord Snall [b], Anne Sverdrup-Thygeson [a]

[a] Faculty of Environmental Sciences and Natural Resource Management, Norwegian University of Life Sciences, Ås, Norway
[b] Swedish Species Information Centre, Swedish University of Agricultural Sciences, Uppsala, Sweden
[c] Field Station Fabrikschleichach, Department of Animal Ecology and Tropical Biology, Biocenter, University of Würzburg, Glashüttenstraße 5, 96181 Rauhenebrach, Germany
[d] Bavarian Forest National Park, Freyunger Str. 2, 94481 Grafenau, Germany
[e] Organismal and Evolutionary Biology Research Programme, University of Helsinki, Helsinki, Finland
[f] Department of Biological and Environmental Science, P.O. Box 35, 40014 University of Jyväskylä, Finland
[g] Natural History Museum, University of Oslo, Oslo, Norway

ARTICLE INFO

Keywords:
Coleoptera
Indicator species
Joint species distribution models (JSDMs)
Near-natural forest
Red-listed species
Saproxylic beetles

ABSTRACT

Wood-living beetles make up a large proportion of forest biodiversity and contribute to important ecosystem services, including decomposition. Beetle communities in managed southern boreal forests are less species rich than in natural and near-natural forest stands. In addition, many beetle species rely primarily on specific tree species. Yet, the associations between individual beetle species, forest management category, and tree species are seldom quantified, even for red-listed beetles. We compiled a beetle capture dataset from flight intercept traps placed on Norway spruce (*Picea abies*), oak (*Quercus* sp.), and Eurasian aspen (*Populus tremulae*) trees in 413 sites in mature managed forest, near-natural forest, and clear-cuts in southeastern Norway. We used joint species distribution models to estimate the strength of associations for 368 saproxylic beetle species (including 20 vulnerable, endangered, or critical red-listed species) for each forest management category and tree species. Tree species on which traps were mounted had the largest effect on beetle communities; oaks had the most highly associated beetle species, including most of the red-listed species, followed by Norway spruce and Eurasian aspen. Most beetle species were more likely to be captured in near-natural than in mature managed forest. Our estimated associations were compatible – for many species – with categorical classifications found in several existing databases of saproxylic beetle preferences. These quantitative beetle-habitat associations will improve future analyses that have typically relied on categorical classifications. Our results highlight the need to prioritize conservation of near-natural forests and oak trees in Scandinavia to protect the habitat of many red-listed species in particular. Furthermore, we underline the importance of carefully considering the species of trees on which traps are mounted in order to representatively sample beetle communities in forest stands.

1. Introduction

Wood-living (saproxylic) beetles are of particular importance for conservation of forest biodiversity; they are highly diverse and provide important ecosystem services such as decomposition (Ulyshen, 2016). Yet, they are known to be sensitive to intensive forest management due to their reliance on deadwood (Grove, 2002; Müller et al., 2013; Ulyshen, 2018). Mature managed forests harbor fewer beetle species than natural and 'near-natural' forests, which have never been clear-cut and in which no recent management actions have taken place (Hjältén et al., 2012; Kraut et al., 2016; Hilmers et al., 2018; Jacobsen et al., 2020). Little is known about the effects of management on most individual species, and some species are likely much more sensitive than even these overall richness patterns suggest. The quality of managed forests also varies throughout their lifespan; clear-cuts briefly harbor increased beetle richness, for example, including many species that are excluded from managed forests when they mature (Similä et al., 2002).

Boreal forest ecosystems make up nearly a third of Earth's forest

* Corresponding author.
E-mail address: ryan.c.burner@gmail.com (R.C. Burner).

https://doi.org/10.1016/j.foreco.2021.119023
Received 11 November 2020; Received in revised form 28 January 2021; Accepted 30 January 2021
Available online 16 February 2021

cover and are important for biodiversity, carbon storage, and forest products (Gauthier et al., 2015). Management intensification in this region, however, can have negative impacts on biodiversity. Forest management practices, which change many forest characteristics such as tree age, structural heterogeneity, amount of deadwood, and forest patch size (Penttilä et al., 2004; Regnery et al., 2013; Heikkala et al., 2016; Ameztegui et al., 2018), affect the suitability of these forests for many species (Heikkala et al., 2016; Laaksonen et al., 2020). At the same time, society increasingly values forest biodiversity (Borrass et al., 2017).

Forest management not only impacts forest structure but also causes changes in tree species composition, including reducing the proportion of deciduous trees in mixed southern boreal forests (Martikainen et al., 2000; Schelhaas et al., 2003; Vanha-Majamaa et al., 2007). This is important for wood-living beetle species, because many of them are associated with certain tree species. Management intensification homogenizes forest communities and shifts tree species composition away from mixed forests, which also contain deciduous trees, towards spruce monocultures (Gauthier et al., 2015). These changes mean that it is increasingly important to quantify and understand beetle species' requirements. This is particularly true for red-listed species, many of which are linked to tree species like oaks that are not favored in current management priorities (Koch Widerberg et al., 2012).

Many saproxylic beetle species are associated not only with certain tree species, but also with certain forest management categories (Hjältén et al., 2012; Müller et al., 2015). Although differences in overall beetle species richness among different management categories have been well documented, current understanding of the sensitivity of saproxylic boreal forest beetle species to intensive forest management is based primarily on expert opinion (Dahlberg and Stokland, 2004; Dahlberg, 2011; Seibold et al., 2015), although experimental approaches are becoming more common in central Europe (Müller et al., 2015; Müller et al., 2020; Vogel et al., 2020). Yet, these qualitative lists of beetle-management category and beetle-tree associations, even if helpful and accurate, may mask large differences in the strengths of beetle-habitat associations among saproxylic species. Furthermore, host tree associations can differ depending on management practices and geographic area (Müller et al., 2015). Hence, it is increasingly important to quantify the actual strength of association, preferentially within the natural context.

To quantitatively estimate the associations between wood-living beetle species, several tree species, and several forest management types, we compiled a dataset of wood-living beetle captures from flight intercept traps placed on Norway spruce (*Picea abies*), oaks (*Quercus* sp.), and Eurasian aspen (*Populus tremulae*) trees in mature managed forests, near-natural forests, and clear-cuts in southeastern Norway. We asked:

(a) What is the strength of associations between beetle species and each of several tree species and forest management categories?
(b) To what extent is each beetle species associated with certain forest management categories and tree species?
(c) Are red-listed beetle species more likely to be associated with certain tree species or forest management categories, and which of each are most important?

2. Methods

2.1. Beetle sampling

We compiled data from past work (Burner et al., 2020; Jacobsen et al., 2020) in which we used flight intercept traps to sample beetles in 413 sites in southeastern Norway (Fig. 1). Flight intercept traps were placed in three forest management categories (mature managed forest, recent clear-cuts, and near-natural forests) and hung in Norway spruce (*Picea abies*), Eurasian aspen (*Populus tremulae*), and oaks (*Quercus* sp.) trees (hereafter 'trap tree'), as well as free-hanging. The spruce and aspen trees in which traps were hung were all located in coniferous-dominated southern boreal forest, typically dominated by spruce and pine, but with some (mostly boreal) deciduous tree species. The oaks in which traps were hung were typically further south in Norway, in forests with a mix of coniferous and deciduous trees. Proportions of each trap tree were roughly comparable among the forest management categories (Supplemental table S1). Sampling took place from 1998 to 2019, with traps deployed from May to August and emptied several times during this period. All samples from a given trap in a given year were pooled for sampling. Sites were sampled for a mean of 2.5 years each, for a total of

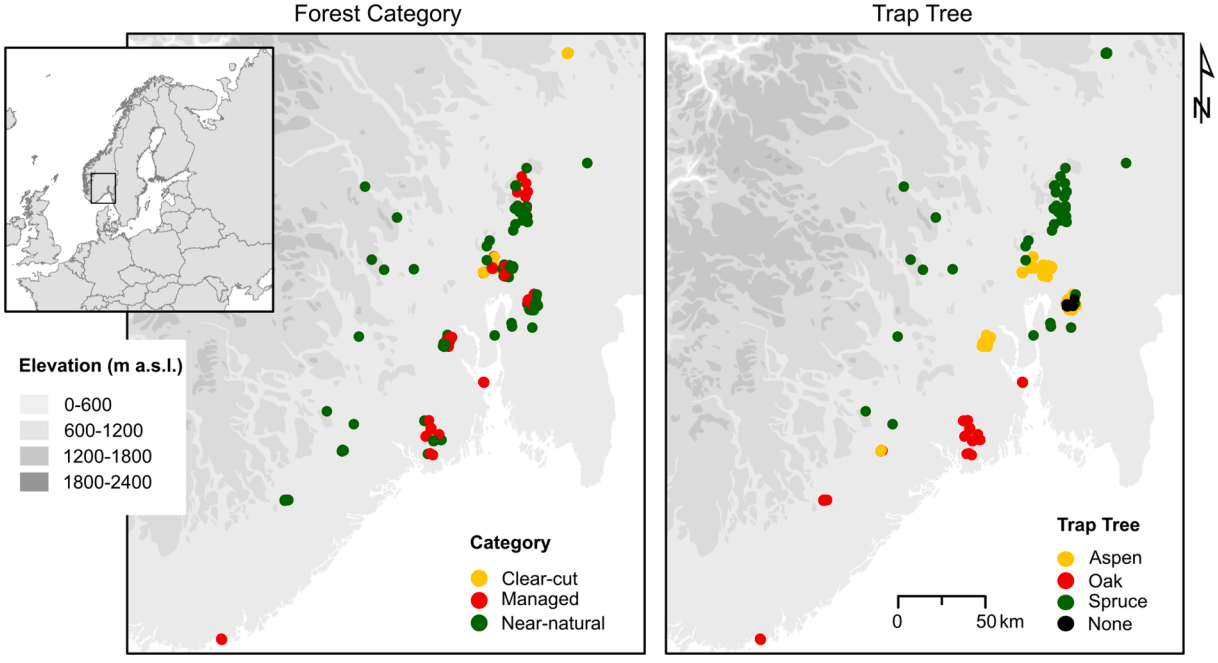

Fig. 1. Map of beetle capture sites in southeast Norway, showing forest management category (left) and trap tree (right) at each site. Inset map shows location in northern Europe.

1029 samples (Table S2) and median distance to nearest neighbor among sites was 167 m. Most of the managed forest and clear-cut sites were managed as sustainable production forests within the regulations of the PEFC (the Programme for the Endorsement of Forest Certification schemes, Norway, pefcnorway.org). Our near-natural forests have never been clear-cut, are heterogeneous in horizontal and vertical structure, and have older trees and higher deadwood volumes compared to managed forest (Storaunet et al., 2005; Jacobsen et al., 2020).

Beetles were identified to species (taxonomy follows GBIF; gbif.org) and categorized as red-listed according to the Norwegian Red List (Henriksen and Hilmo, 2015). We included wood-living species that were captured in four or more sites (n = 368), including facultative and obligate wood-living species based on the Saproxylic Database (Dahlberg and Stokland, 2004), in our analyses. We also extracted species' host tree preferences (Dahlberg and Stokland, 2004) and natural forest association classifications (Dahlberg, 2011) from these databases to compare them with our quantitative estimates.

2.2. Analysis

To test for associations between beetle species, forest management categories, and trap tree species, we applied hierarchical Bayesian joint species distribution modelling (Ovaskainen et al., 2017; Ovaskainen and Abrego, 2020). We fitted a set of three models to examine the differences in beetle species captured among different trap tree species and forest management categories. The first of these three models included trap tree species as a categorical fixed effect, the second one had forest management category as a fixed effect, and in the third model we included both of these sets of fixed effect covariates. We used the full presence/absence dataset and assumed a Bernoulli distribution and a probit link function. One sampling unit consisted of one trap deployed for an entire summer. To account for the temporal structure in our study design, in which many sites were sampled in multiple years, each model included site as a random effect. This random effect of site estimates a common intercept for all sampling years at a given site, because most sites were sampled in multiple years. To test for correlations between species' phylogeny and their responses to the covariates, we also included a random effect of phylogeny based on the species-level insect tree by Chesters (2017); missing species were added at random to the correct genus (where present) or in several cases to the correct family using package *phytools* (Revell, 2012). Models were fitted using a Gibbs sampler using the default prior distributions from package *Hmsc* (Tikhonov et al., 2020) in R (R Core Team, 2019).

Model fitting was conducted with high performance computational resources provided by Louisiana State University (http://www.hpc.lsu.edu). We sampled the posterior distribution with three MCMC chains, each running for 5000 iterations, of which 2500 were discarded as burn-in. Every fifth iteration was sampled from the remaining iterations, resulting in 500 samples per chain. Convergence was assessed by calculating effective sample size and the potential scale reduction factor, as well as by visual inspection of the MCMC trace plots. Final models had 95% of scale reduction factors below 1.2, with a median value of 1.01. We compared models using Tjur R^2 values from two-fold cross validation (folded on trap site) to rank models.

To assess the strength of the associations between each species and the various trap trees and forest management categories, we used the best fitting mode for the community to predict beetle communities at 2400 hypothetical new sites. These included 800 sites in each forest management category; of each of those sets of 800, there were 200 sites with each species of trap tree, as well as 200 sites with free-hanging traps. The large number of sites was used to make sure that rare species occurred sufficiently often in the simulated communities to calculate their habitat associations with adequate precision. Model predictions are more easily interpretable than are parameter estimates for a single covariate because predictions incorporate information from all fixed and random effects in the model (Purhonen et al., 2019). We repeated these predictions 1500 times using draws from the joint posterior distribution of the model parameters.

In order to obtain relative association scores between a given beetle species and each of the three trap tree types (oak, aspen, and spruce), we calculated the proportion of sites occupied by that beetle species for each of the three trap tree types in a given predicted iteration. We then scaled these three proportions such that they summed to one to provide a relative association score (Rutt et al., 2019) that was comparable among species that differed in their occupancy rates. We repeated this process for each of the 1500 predicted iterations, such that the resulting scaled values represented the posterior distributions of these relative association scores. We calculated these values for each beetle species; a score of zero for a given trap tree type thus indicates that that particular beetle species is never predicted to be captured there, and a score of one indicates that the beetle species should be trapped exclusively in that type of tree. A score of 0.333 indicates that a given beetle species is no more (or less) associated with a given trap tree than expected by chance. This facilitated three-way comparisons and plotting (Smith, 2017). Species with 95% credible intervals (CIs) above 0.333 for one or more tree types are considered specialists.

To calculate relative association scores for beetle species with mature managed and near-natural forest categories we used a similar approach, calculating the proportion of sites occupied in each of these two forest management categories and scaling them to sum to one. In this case a natural forest association score of 1 indicates that the beetle species occurs only in natural forest, whereas a score of 0.5 indicates no association with either forest management category. A score of 0 indicates that the beetle species occurs only in managed forests. Species with 95% CIs above 0.5 for either forest management category are considered specialists. We focus primarily on results from this two-way comparison, rather than from a three-way comparison that includes clear-cuts because we lack comparable reference trap sites in smaller natural openings that occur in unmanaged forests. Such natural openings are the natural forest analog of clear-cut sites, and would be needed to assess the relative associations between early successional beetle species and managed vs. natural forest. Nevertheless, we also include a supplemental analysis of three-way association scores (managed, near-natural, and clear-cut; see supplemental material) because this does provide some indication of the proportion of wood-living beetle species that rely on early successional stages.

3. Results

The model that included both trap tree and forest management category covariates performed the best, based on predictive Tjur R^2 values (Table 1). In comparing models with only one of these covariates,

Table 1
Joint species distribution models fitted to a wood-living beetle dataset from southeastern Norway. The trap tree covariate included four levels (Aspen, Oak, Spruce, and free-hanging), and forest management category included three levels (mature managed, clear-cut, and near-natural forest).

Environmental covariates	Variance partitioning of fixed effects*	Mean explanatory Tjur R^2**	Mean predictive Tjur R^2**
Trap tree + forest management category	0.51	0.158	0.055
Trap tree	0.42	0.154	0.042
Forest management category	0.16	0.156	0.012

* Variance partitioning of fixed effects shows how much of the model's explanatory power can be attributed to environmental covariates (the fixed effects), as opposed to the random effect of site.

** Mean explanatory Tjur R^2 refers to the mean of all species' R^2 values in the full fitted model. Mean predictive R^2 refers to the R^2 value of the model after two-fold cross-validation, folded over the sampling units.

the trap tree model outperformed the forest management category model. There was a moderately strong signal of phylogenetic effects in species responses to the covariates (95% CI: 0.28–0.59).

Many species showed strong associations with a single tree type (Fig. 2). Of 368 species, 151 (41%) were predicted to have over half of their captures in one type of tree (with at least 95% posterior support). Oak had the greatest number of such associated species (n = 96), followed by spruce (n = 48) and aspen (n = 7). Oak also had a large number of very strongly associated species, including 53 species with over 80% of their predicted occurrences in oak. Association scores for each species are shown in Table S3. Of 20 red-listed species, five were predicted to be trapped most often in spruce and 13 were predicted to occur exclusively on oaks. Among trap trees, species richness was predicted to be similar (95% CI) for traps placed on oak and spruce trees (means = 31.4 and 33.6 species, respectively; Fig. S1) in natural forest. Predicted richness on aspen trees was 11.9 species lower than on spruce (95% CI: 4.4–19.5). Among forest management categories, species richness was predicted to be 33.4 species for traps placed in near natural forest, and 1.3–8.5 species lower for traps in mature managed forests (95% CI; Fig. S2).

Most species (n = 260, 70.7%) were more likely to be captured in near-natural forest (mean association score of all species = 0.56 on a scale from 0 to 1; Fig. 3) than in natural forest. For almost half of all species (n = 136, 37.0%) the 50% CI indicated a positive association with natural forest, compared with only 25 species (6.8%) in managed forest. More conservative estimates are that 7.3% (27) and 0.8% (three) of the species are associated with natural and managed forests, respectively, as judged by the overlap of zero by the 95% CIs. Beetle species that were positively associated with oak trees have the highest mean natural forest association scores (μ = 0.60; Fig. S3), followed by spruce (μ = 0.55) and aspen (μ = 0.49). All means differed (95% CI). Mean natural forest association score of red-listed species was 0.03 higher than other species (95% CI: −0.02 – 0.08).

When we considered forest management category associations

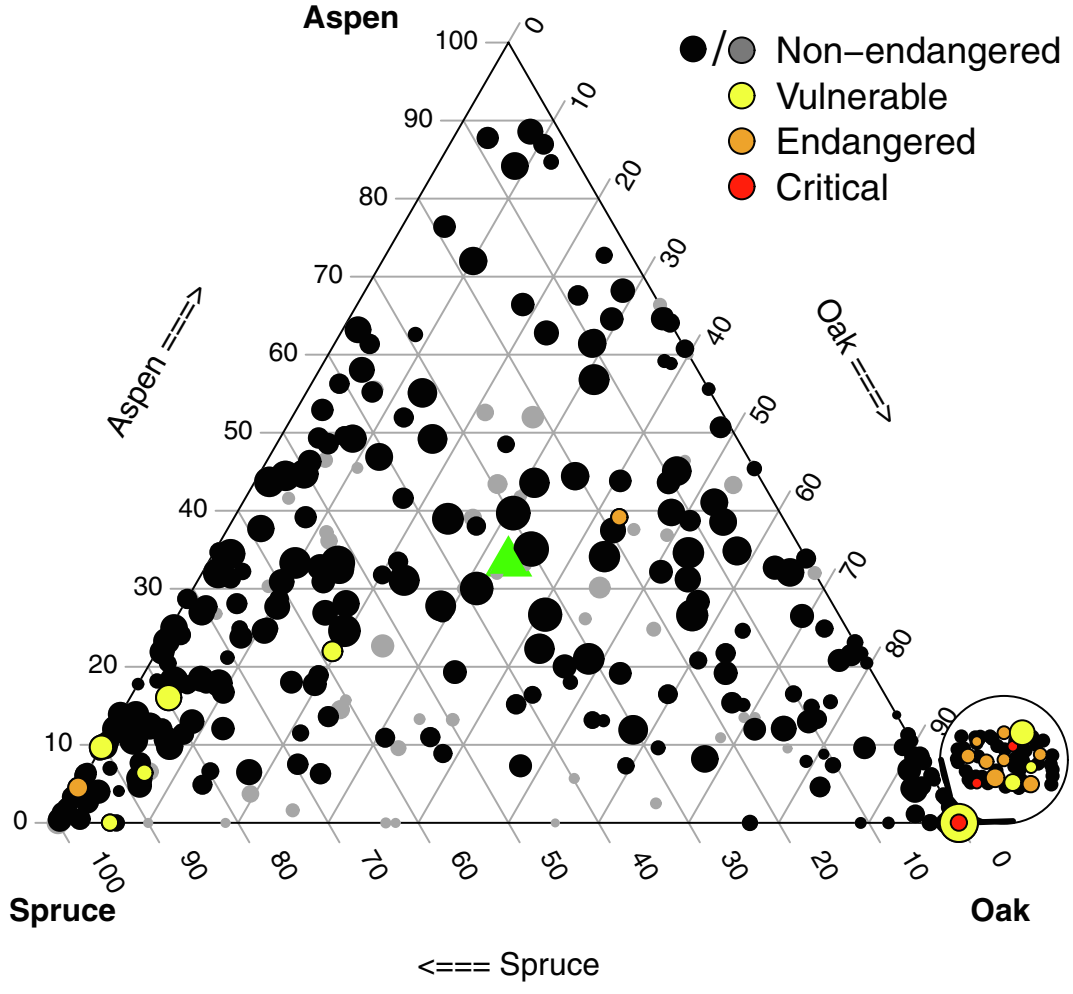

Fig. 2. Relative association scores of wood-living beetle species with the three tree species on which traps were mounted. Black points represent 'specialist' species, which have 95% credible intervals that reflect association with one or more tree species (i.e. have posterior intervals that do not overlap the plot center, which is marked by a green triangle). Species represented by grey points are not associated with any trap tree (95% CI). Each point represents the median estimate for a single beetle species, and the size of the point is proportional to the species' log-transformed prevalence in the whole dataset. Red-listed species are colored according to their red-list category and have their relative size doubled for visibility; all red-listed species have posterior intervals that exclude the plot center with the exception of the yellow and orange dots just left and right of the center, respectively. Points closer to the plot corners have strong associations with a single trap tree. Many red-listed species are clustered in the oak corner, as are an additional 47 specialist species that are not on the Norwegian Red List (see jittered points in zoomed inset). (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

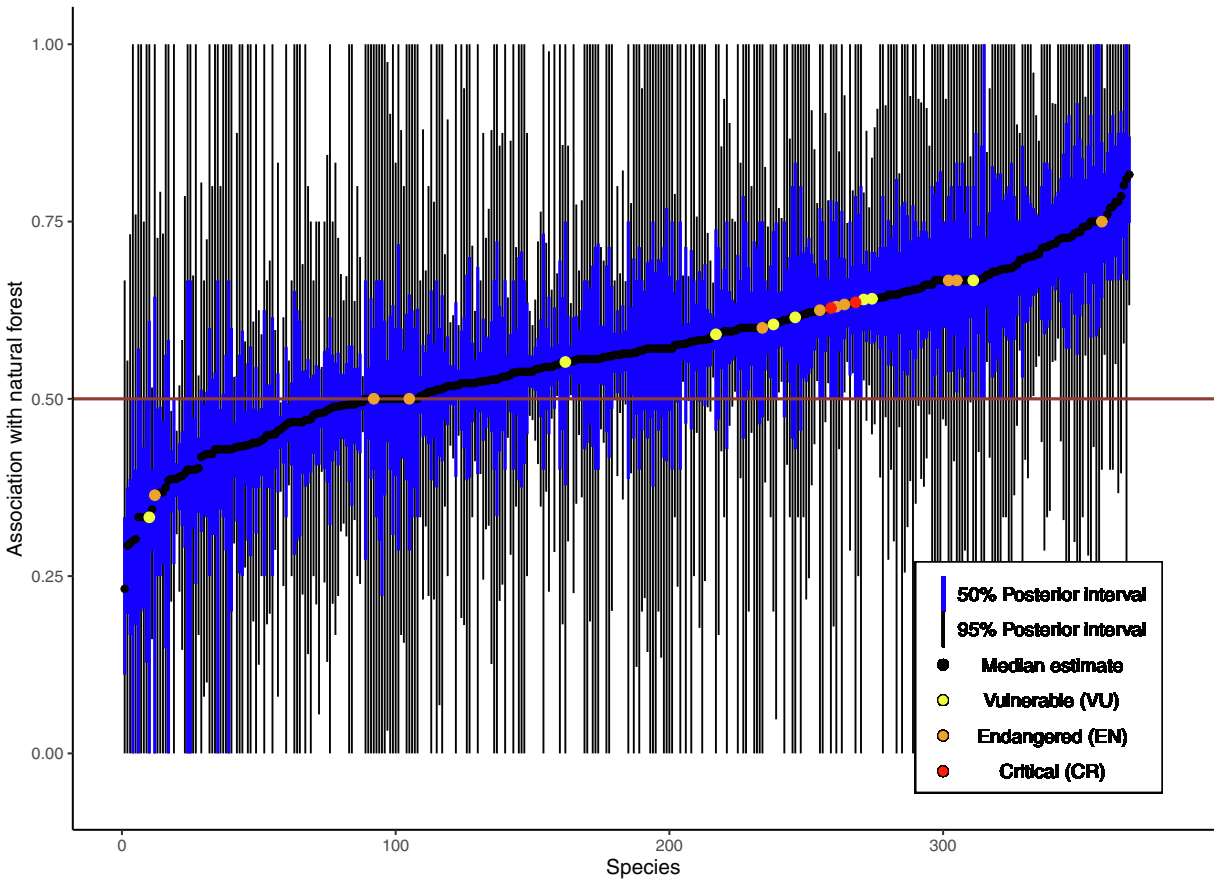

Fig. 3. Predicted near-natural forest association scores for 368 wood-living beetle species from southeastern Norway. A score of '1' indicates that all captures are predicted to occur in near-natural forests, a score of '0.5' means to be trapped in mature managed or near-natural forest, and a score of '0' indicates that all captures are predicted to occur in near-natural forests. Values are estimated from Bayesian joint species distribution models (JSDMs) that include both forest management category and trap tree species as fixed effects. Species that occur on the Norwegian Red List (Henriksen and Hilmo, 2015) are marked as indicated. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

including clear-cuts (a 3-way comparison), some species were also positively associated with clear-cuts (Fig. S4 and Table S3). Of 131 species that had 95% CIs favoring one or more forest management categories, 58 (44.3%) species were predicted to have over half of their occurrences in clear-cuts, 34 (26.0%) species in natural forests, and no species in mature managed forests.

Species considered by Dahlberg (2011) to be associated, highly associated, and non-associated with natural forest did not differ in their mean natural forest association scores (95% CIs; Fig. S5). Our estimated tree associations for many beetle species correspond to those indicated by the Saproxylic Database (Dahlberg and Stokland, 2004). Of 141 species listed as using or preferring conifers that were included in our dataset, we found that 51% were associated with conifers, 24% with deciduous trees, and 25% had no clear association (95% CI). Of 137 species listed as using or preferring deciduous trees, we found that 60% were associated with deciduous trees, 12% with conifers, and 28% had no clear association (Table 2).

4. Discussion

We found a stronger relationship between beetle species occurrences and individual tree species than with different forest management categories, although both had strong effects. Most of the beetle species were most likely to occur in near-natural forest and very few species were most likely to occur in mature managed forests (Figs. 2 and 3). Among tree species, oaks had more apparent specialist species (species found to disproportionately occur on them) than did spruce, and both had many more than aspen. Red-listed species were slightly more strongly

Table 2
Relationship between expert-derived host tree preferences of 368 wood-living beetle species (columns) from the Saproxylic Database (Dahlberg and Stokland, 2004) and median estimated tree association scores from our joint species distribution model (rows). Values represent the number of species. In the Saproxylic Database, species are classified as either 'using' or 'preferring' deciduous or coniferous trees. Species preferring either oaks, aspen, or a mix of both from our model were combined in the deciduous category. Underlined values represent agreement on tree type association between empirical values and the Saproxylic Database.

Model-estimated median association*	Conifers, prefer	Conifers, use	Deciduous, prefer	Deciduous, use	Unknown
Spruce, >2/3	28	25	0	7	8
Spruce, >1/3	9	10	3	6	6
Deciduous, >2/3	4	10	20	44	36
Deciduous, >1/3	9	11	3	15	15
No association	14	21	4	35	25

* Scores from our study, representing % of species captures predicted to occur in a given tree type; species with no association are those for which the 95% credible interval included 0.333 for each tree type (see Fig. 2).

associated with natural forest, and many were captured only on oak trees.

Our finding that four in ten beetle species are strongly associated with one or several tree species in our dataset has important implications for conservation. As forest management intensification has led to a homogenization of forests in Scandinavia, spruce monocultures are increasingly common (Penttilä et al., 2004). This is detrimental to the many oak specialist species, which even prior to the advent of large-scale clear-cut forestry had suffered from a reduction in the abundance and extent of oak trees in the region due to timber demand from shipbuilders (Vevstad, 1998). Red-listed species in particular are threatened by the continued loss of these oak trees (Pilskog et al., 2018). Oaks are concentrated in the southern part of our study area and spatially segregated from our sites with other trap trees, so some beetle species that appear to be associated with oaks could rather simply be more common in this southern region or in stands with a larger proportion of deciduous trees and some additional uncommon deciduous species. But, the strength of apparent specialization of many oak-associated beetles in our models, and the relative similarity of the forest stands in which we sampled each type of trap tree (nearly all stands in our study contained a mixture of some deciduous and coniferous trees), suggest that a large proportion of these beetle species are true oak associates.

Our results contrast with those of Milberg et al. (2014), who detected relatively few strong associations between beetle species and several deciduous tree species in southern Sweden. This difference could result from higher similarities between the larger number of temperate deciduous trees species there, compared to our contrasting mixed deciduous and coniferous temperate and boreal tree species in Norway. Our dataset lacked traps set in birch (*Betula sp*.) and pine (*Pinus sp*.), two other tree species common in boreal forests, so it is possible that some of our apparent specialist beetles on sampled tree species also occur on these other trees. Pine and birch likely also have specialists of their own that we missed with our current sampling (Jonsell et al., 2004). Nevertheless, we show strong positive (and negative) associations between many beetle species and tree species in southern boreal forests. Very rare species, necessarily excluded from our models, may also exhibit strong associations with one or more tree species or management category.

Forest management category is also an important axis of variation in beetle communities, with many species occurring more commonly in near-natural forests. A clear pattern of natural forest association emerges for the majority of species (Fig. 3); as expected, our CIs are wide because of the large proportion of rare species that is common in biodiversity datasets. This association with near-natural forests fits with previous findings that wood-living beetle communities in near-natural forest are more species rich and have higher abundance (Paillet et al., 2010; Jacobsen et al., 2020). Unlike prior studies, however, we have quantified association scores for 368 species, providing a list of species most likely to be highly sensitive to intensive forest management, including many red-listed species (Table S3).

Species identified as associated with natural forests in Nordic forests based on expert knowledge and reviews of literature (Dahlberg, 2011) were not more highly associated with natural forest than other species in our study, highlighting the need for a quantitative list for use by forest managers. However, we found that many of our beetle – tree association estimates corresponded fairly well to expert opinion-based classifications from Nordic forests in the Saproxylic Database (Dahlberg and Stokland, 2004), although for about one quarter of the species with listed associations that we tested we did not detect any association with tree species; in some cases this may be due simply to our small number of captures of particular species. Our results provide tree species association scores from capture data alone, and should be supplemented with e.g. larval surveys to document the actual use of these trees by various life stages for each species. Qualitative expert opinion is a valuable source of information for poorly known taxa, but empirical validation should be attempted whenever possible. Such sampling should cover the full range of common tree species.

Natural and near-natural forests continue to disappear in Scandinavia (Felton et al., 2019). Conservation of a diverse selection of those remaining forests that have never been clear-cut, including a cessation of management activities to allow them to develop near-natural characteristics (Paillet et al., 2010), should be a priority for nature conservation. In addition to the wildlife species that rely on heterogenous natural stands of these forests, the lack of large expanses of old natural forest make it difficult to study another group - 'gap' species that specialize on natural disturbances within boreal forest landscapes. The presence of a subset of beetle species that occur in our dataset primarily in clear-cuts (Fig. S4) points to the existence of many such gap species, but comparable abundance data from natural forest openings are lacking. Natural openings in unmanaged forest are richer in deadwood than are clear-cuts (Junninen et al., 2006; Djupström et al., 2012; Heikkala et al., 2016), and likely provide better habitat for many of these species. Nonetheless, a subset of these gap species may be more resilient to current stand-replacing forestry techniques than are the majority of beetle species.

It is important to note that our results provide a rather conservative estimate of the true differences between mature managed and natural forests, and thus likely underestimate the associations of most beetle species with natural and near-natural forests. This is because researchers typically select the best (most dead wood rich) sampling sites in managed forest in order to be assured of catching more of the beetle species that occur there, as we have done in the present study. Sampling sites with coarse woody debris are chosen in near-natural forests as well, but because such sites are rarer in mature managed forests (Jonsson et al., 2016) this sampling site selection method likely overestimates the habitat quality of managed forests. Furthermore, with data based on flight intercept trap captures of (mainly adult) beetles rather than on evidence of reproduction, it is possible that managed forests actually act as population sinks for many species that do occur there. The same could be true of clear-cuts, which have smaller and more ephemeral dead wood than do natural forest gaps (Similä et al., 2002; Jonsell and Schroeder, 2014; Heikkala et al., 2016). Further research should examine differences in beetle reproduction at representative sites in managed and natural forests.

In addition to informing conservation priorities, the importance of choice of trap trees should inform research methodology. We do not have precise information on the overall species composition of our sites, although most were in mixed deciduous-coniferous stands, but traps that were hung on one species of tree were likely to surrounded by trees of other species (especially in the case of oak and aspen, which are seldom the dominant tree species). Nevertheless, trap tree identity does to some extent reflect the composition of the surrounding stand (especially perhaps in the case of oaks, which can cooccur with other deciduous species in more temperate parts of Norway), causing us to overestimate the importance of the individual tree on which traps are placed. Also, our association scores simply reflect a correlation between trap tree and capture rates, without demonstrating that a particular tree species is actually the preferred host tree for a given beetle species. That we see such strong effects of trap tree identity in spite of these unknowns is evidence of the strong effects of small-scale processes (on the order of several meters) in determining beetle captures. This finding presents a methodological challenge for future studies, because it means that captures of many beetle species in a given trap may be influenced as much by the species of tree that the trap is mounted on as by the forest stand as a whole (Müller et al., 2018). Additionally, the impact of management activities may differ among species preferring different host trees; a more systematic sampling design would allow for a test for an interaction between trap tree and forest management type.

For studies that seek to understand forest stand level effects, we suggest that traps in each forest stand should be placed on tree species in proportion to their abundance in that forest stand. This is

methodologically challenging, requiring either some forest inventory measurements or complete randomization (which would perhaps require impractically larger sample sizes to ensure that a purely random sample converged on the true distribution of tree species). Another option would be to sample multiple tree species at each site and then test whether results are robust to differences in trap tree selection. At a minimum, studies that have imbalanced designs, in which trap tree is confounded with other variables of interest, should attempt to correct for trap tree species by including it as a covariate in models (as we've done here) along with the other covariates of interest.

5. Conclusions

We have demonstrated the importance of both trap tree identity and forest management category on beetle communities sampled in southern boreal forests. This has important implications both for conservation prioritization and for research methodology. From a conservation perspective, the shift towards even-aged spruce monocultures that has characterized forestry in boreal regions (Schelhaas et al., 2003) is likely damaging to many taxa that rely on other tree species; oak trees (which occur at low densities near their northern range limits in the southern boreal forest) are of particular importance for many obligate oak inhabiting species, including many red-listed beetles. Monocultures may also be less resilient to ongoing bark beetle outbreaks (Dobor et al., 2020). Natural and near-natural forests are also critical for many species and should be given particular attention in conservation management.

CRediT authorship contribution statement

Ryan C. Burner: Conceptualization, Methodology, Formal analysis, Writing - original draft. **Tone Birkemoe:** Conceptualization, Methodology, Funding acquisition, Writing - original draft. **Jörg G. Stephan:** Methodology, Writing - review & editing. **Lukas Drag:** Methodology, Writing - review & editing. **Jörg Muller:** Writing - review & editing. **Otso Ovaskainen:** Methodology, Writing - review & editing. **Mária Potterf:** Writing - review & editing. **Olav Skarpaas:** Methodology, Writing - review & editing. **Tord Snall:** Funding acquisition, Supervision, Writing - review & editing. **Anne Sverdrup-Thygeson:** Conceptualization, Methodology, Funding acquisition, Supervision, Writing - original draft.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Data availability

Data are available on Zenodo: https://doi.org/10.5281/zenodo.4475536.

Acknowledgements

This research was funded through the 2017–2018 Belmont Forum and BiodivERsA joint call for research proposals, under the BiodivScen ERA-Net COFUND programme, for "BioESSHealth: Scenarios for biodiversity and ecosystem services acknowledging health", and with the funding organizations NFR (grant no. 295621), Formas (grant no. 2018-2435), and DLR. Thanks also to Sindre Ligaard for identifying the beetle species, and to numerous field assistants who set and maintained traps.

Appendix A. Supplementary material

Supplementary data to this article can be found online at https://doi.org/10.1016/j.foreco.2021.119023.

References

Ameztegui, A., Gil-Tena, A., Faus, J., Piqué, M., Brotons, L., Camprodon, J., 2018. Bird community response in mountain pine forests of the Pyrenees managed under a shelterwood system. For. Ecol. Manage. 407, 95–105.
Borrass, L., Kleinschmit, D., Winkel, G., 2017. The "German model" of integrative multifunctional forest management—Analysing the emergence and political evolution of a forest management concept. For. Policy Econ. 77, 16–23.
Burner, R.C., Birkemoe, T., Olsen, S.L., Sverdrup-Thygeson, A., 2020. Sampling beetle communities: Trap design interacts with weather and species traits to bias capture rates. Ecol. Evol. 10, 14300–14308.
Chesters, D., 2017. Construction of a species-level tree of life for the insects and utility in taxonomic profiling. Syst. Biol. 66, 426–439.
Dahlberg, A., 2011. Kontinuitetsskogar och hyggesfritt skogsbruk: Slutrapport för delprojekt naturvärden. Skogsstyrelsen, Swedish Forest Agency, Jönköping, Report 7, 1100-0295.
Dahlberg, A., Stokland, J.N., 2004. Vedlevande arters krav på substrat – en sammanställning och analys av 3600 arter (Substrate requirements of wood-inhabiting species – a synthesis and analysis of 3600 species). In: In Swedish with English summary, Skogsstyrelsen, Report 7, Jönköping.
Djupström, L.B., Weslien, J., Hoopen, J.T., Schroeder, L.M., 2012. Restoration of habitats for a threatened saproxylic beetle species in a boreal landscape by retaining dead wood on clear-cuts. Biol. Conserv. 155, 44–49.
Dobor, L., Hlásny, T., Zimová, S., 2020. Contrasting vulnerability of monospecific and species-diverse forests to wind and bark beetle disturbance: The role of management. Ecol. Evol. 10, 12233–12245.
Felton, A., Löfroth, T., Angelstam, P., Gustafsson, L., Hjältén, J., Felton, A.M., Simonsson, P., Dahlberg, A., Lindbladh, M., Svensson, J., Nilsson, U., Lodin, I., Hedwall, P.O., Sténs, A., Lämås, T., Brunet, J., Kalén, C., Kriström, B., Gemmel, P., Ranius, T., 2019. Keeping pace with forestry: Multi-scale conservation in a changing production forest matrix. Ambio 49, 1050–1064.
Gauthier, S., Bernier, P., Kuuluvainen, T., Shvidenko, A.Z., Schepaschenko, D.G., 2015. Boreal forest health and global change. Science 349, 819–822.
Grove, S.J., 2002. Saproxylic insect ecology and the sustainable management of forests. Annu. Rev. Ecol. Syst. 33, 1–23.
Heikkala, O., Seibold, S., Koivula, M., Martikainen, P., Müller, J., Thorn, S., Kouki, J., 2016. Retention forestry and prescribed burning result in functionally different saproxylic beetle assemblages than clear-cutting. For. Ecol. Manage. 359, 51–58.
Henriksen, S., Hilmo, O., 2015. The 2015 Norwegian red list for species. Norwegian Biodiversity Information Centre, Norway.
Hilmers, T., Friess, N., Bässler, C., Heurich, M., Brandl, R., Pretzsch, H., Seidl, R., Müller, J., 2018. Biodiversity along temperate forest succession. J. Appl. Ecol. 55, 2756–2766.
Hjältén, J., Stenbacka, F., Pettersson, R.B., Gibb, H., Johansson, T., Danell, K., Ball, J.P., Hilszczański, J., 2012. Micro and macro-habitat associations in saproxylic beetles: implications for biodiversity management. PLoS ONE 7, e41100.
Jacobsen, R.M., Burner, R.C., Olsen, S.L., Skarpaas, O., Sverdrup-Thygeson, A., 2020. Near-natural forests harbor richer saproxylic beetle communities than those in intensively managed forests. For. Ecol. Manage. 466, 118124.
Jonsell, M., Nittérus, K., Stighäll, K., 2004. Saproxylic beetles in natural and man-made deciduous high stumps retained for conservation. Biol. Conserv. 118, 163–173.
Jonsell, M., Schroeder, M., 2014. Proportions of saproxylic beetle populations that utilise clear-cut stumps in a boreal landscape – Biodiversity implications for stump harvest. For. Ecol. Manage. 334, 313–320.
Jonsson, B.G., Ekström, M., Esseen, P.-A., Grafström, A., Ståhl, G., Westerlund, B., 2016. Dead wood availability in managed Swedish forests – Policy outcomes and implications for biodiversity. For. Ecol. Manage. 376, 174–182.
Junninen, K., Similä, M., Kouki, J., Kotiranta, H., 2006. Assemblages of wood-inhabiting fungi along the gradients of succession and naturalness in boreal pine-dominated forests in Fennoscandia. Ecography 29, 75–83.
Koch Widerberg, M., Ranius, T., Drobyshev, I., Nilsson, U., Lindbladh, M., 2012. Increased openness around retained oaks increases species richness of saproxylic beetles. Biodivers. Conserv. 21, 3035–3059.
Kraut, A., Liira, J., Löhmus, A., 2016. Beyond a minimum substrate supply: Sustaining saproxylic beetles in semi-natural forest management. For. Ecol. Manage. 360, 9–19.
Laaksonen, M., Punttila, P., Siitonen, J., Ovaskainen, O., 2020. Saproxylic beetle assemblages in recently dead Scots pines: How traits modulate species' response to forest management? For. Ecol. Manage. 473, 118300.
Martikainen, P., Siitonen, J., Punttila, P., Kaila, L., Rauh, J., 2000. Species richness of Coleoptera in mature managed and old-growth boreal forests in southern Finland. Biol. Conserv. 94, 199–209.
Milberg, P., Bergman, K.-O., Johansson, H., Jansson, N., 2014. Low host-tree preferences among saproxylic beetles: a comparison of four deciduous species. Insect Conserv. Div. 7, 508–522.
Müller, J., Jarzabek-Müller, A., Bussler, H., 2013. Some of the rarest European saproxylic beetles are common in the wilderness of northern Mongolia. J. Insect Conserv. 17, 989–1001.
Müller, J., Ulyshen, M., Seibold, S., Cadotte, M., Chao, A., Bässler, C., Vogel, S., Hagge, J., Weiß, I., Baldrian, P., Tláskal, V., Thorn, S., 2020. Primary determinants of communities in deadwood vary among taxa but are regionally consistent. Oikos 129, 1579–1588.
Müller, J., Varandi, H.B., Babaii, M.R., Farashiani, M.E., Sageb-Talebi, K., Lange, F., Gossner, M.M., Jarzabek-Müller, A., Roth, N., Thorn, S., Seibold, S., 2018. The diversity of saproxylic insects (Coleoptera, Heteroptera) on four tree species of the Hyrcanian forest in Iran. J. Insect Conserv. 22, 607–625.

Müller, J., Wende, B., Strobl, C., Eugster, M., Gallenberger, I., Floren, A., Steffan-Dewenter, I., Linsenmair, K.E., Weisser, W.W., Gossner, M.M., 2015. Forest management and regional tree composition drive the host preference of saproxylic beetle communities. J. Appl. Ecol. 52, 753–762.
Ovaskainen, O., Abrego, N., 2020. Joint Species Distribution Modelling: With Applications in R. Cambridge University Press.
Ovaskainen, O., Tikhonov, G., Norberg, A., Guillaume Blanchet, F., Duan, L., Dunson, D., Roslin, T., Abrego, N., 2017. How to make more out of community data? A conceptual framework and its implementation as models and software. Ecol. Lett. 20, 561–576.
Paillet, Y., Bergès, L., Hjältén, J., Ódor, P., Avon, C., Bernhardt-Römermann, M., Bijlsma, R.-J., De Bruyn, L., Fuhr, M., Grandin, U., 2010. Biodiversity differences between managed and unmanaged forests: meta-analysis of species richness in Europe. Conserv. Biol. 24, 101–112.
Penttilä, R., Siitonen, J., Kuusinen, M., 2004. Polypore diversity in managed and old-growth boreal Picea abies forests in southern Finland. Biol. Conserv. 117, 271–283.
Pilskog, H.E., Sverdrup-Thygeson, A., Evju, M., Framstad, E., Birkemoe, T., 2018. Long-lasting effects of logging on beetles in hollow oaks. Ecol. Evol. 8, 10126–10137.
Purhonen, J., Ovaskainen, O., Halme, P., Komonen, A., Huhtinen, S., Kotiranta, H., Læssøe, T., Abrego, N., 2019. Morphological traits predict host-tree specialization in wood-inhabiting fungal communities. Fungal Ecology 100863.
R Core Team, 2019. R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. http://www.R-project.org.
Regnery, B., Couvet, D., Kubarek, L., Julien, J.-F., Kerbiriou, C., 2013. Tree microhabitats as indicators of bird and bat communities in Mediterranean forests. Ecol. Ind. 34, 221–230.
Revell, L.J., 2012. phytools: an R package for phylogenetic comparative biology (and other things). Methods Ecol. Evol. 3, 217–223.
Rutt, C.L., Midway, S.R., Jirinec, V., Wolfe, J.D., Stouffer, P.C., 2019. Examining the microclimate hypothesis in Amazonian birds: indirect tests of the 'visual constraints' mechanism. Oikos 128, 798–810.
Schelhaas, M.-J., Nabuurs, G.-J., Schuck, A., 2003. Natural disturbances in the European forests in the 19th and 20th centuries. Glob. Change Biol. 9, 1620–1633.
Seibold, S., Brandl, R., Buse, J., Hothorn, T., Schmidl, J., Thorn, S., Müller, J., 2015. Association of extinction risk of saproxylic beetles with ecological degradation of forests in Europe. Conserv. Biol. 29, 382–390.
Similä, M., Kouki, J., Martikainen, P., Uotila, A., 2002. Conservation of beetles in boreal pine forests: the effects of forest age and naturalness on species assemblages. Biol. Conserv. 106, 19–27.
Smith, M.R., 2017. Ternary: An R Package for Creating Ternary Plots. Zenodo. https://doi.org/10.5281/zenodo.1068996.
Storaunet, K.O., Rolstad, J., Gjerde, I., Gundersen, V.S., 2005. Historical logging, productivity, and structural characteristics of boreal coniferous forests in Norway. Silva Fennica 39, 429.
Tikhonov, G., Opedal, Ø.H., Abrego, N., Lehikoinen, A., de Jonge, M.M.J., Oksanen, J., Ovaskainen, O., 2020. Joint species distribution modelling with the r-package Hmsc. Meth. Ecol. Evol. 11, 442–447.
Ulyshen, M.D., 2016. Wood decomposition as influenced by invertebrates. Biol. Rev. 91, 70–85.
Ulyshen, M.D. (Ed.), 2018. Saproxylic insects: diversity, ecology and conservation. Springer, Heidelberg.
Vanha-Majamaa, I., Lilja, S., Ryömä, R., Kotiaho, J.S., Laaka-Lindberg, S., Lindberg, H., Puttonen, P., Tamminen, P., Toivanen, T., Kuuluvainen, T., 2007. Rehabilitating boreal forest structure and species composition in Finland through logging, dead wood creation and fire: The EVO experiment. For. Ecol. Manage. 250, 77–88.
Vevstad, A., 1998. Agderskog, Agder skogeierlag 1948–1998 og om skog og skogbruk på Agder gjennom tidene. Agder Skogeigarlag, Kristiansand, Norway.
Vogel, S., Gossner, M.M., Mergner, U., Müller, J., Thorn, S., 2020. Optimizing enrichment of deadwood for biodiversity by varying sun exposure and tree species: An experimental approach. J. Appl. Ecol. 57, 2075–2085.