Biodiversity responses to forest management abandonment in boreal and temperate forest ecosystems: A meta-analysis reveals an interactive effect of time since abandonment and climate

Joseph Langridge, Sylvain Delabye, Olivier Gilg, Yoan Paillet, Yorick Reyjol, Romain Sordello, Julien Touroult, Frédéric Gosselin

HAL Id: hal-04553773
https://hal.inrae.fr/hal-04553773

Submitted on 22 Apr 2024

Contents lists available at ScienceDirect

Biological Conservation

Review

Biodiversity responses to forest management abandonment in boreal and temperate forest ecosystems: A meta-analysis reveals an interactive effect of time since abandonment and climate

Joseph Langridge [a,b,*], Sylvain Delabye [c,d,e], Olivier Gilg [f,g], Yoan Paillet [h], Yorick Reyjol [a], Romain Sordello [a], Julien Touroult [a], Frédéric Gosselin [c]

[a] PatriNat (OFB-MNHN-CNRS-IRD), 36 rue Geoffroy-Saint-Hilaire CP41, 75005 Paris, France
[b] Fondation pour la Recherche sur la Biodiversité, Centre de Synthèse et d'Analyse sur la Biodiversité (FRB-Cesab), la Maison des Océans, 195 rue Saint-Jacques, Paris, France
[c] INRAE, UR EFNO, F-45290 Nogent-sur-Vernisson, France
[d] Departments of Ecology and Zoology, Faculty of Science, Charles University, Viničná 7, 12844 Prague, Czechia
[e] Institute of Entomology, Biology Centre, Czech Academy of Sciences, Branišovská 31, 37005 České Budějovice, Czechia
[f] Réserves Naturelles de France (RNF), 2 allée Pierre Lacroute, 21000 Dijon, France
[g] UMR 6249 Chrono-environnement, CNRS, Université de Franche-Comté, 25000 Besançon, France
[h] Université Grenoble-Alpes, INRAE, Lessem, 2 rue de la Papeterie, BP 76-38042 Saint-Martin-d'Hères Cedex, France

ARTICLE INFO

ABSTRACT

Growing evidence suggests that forest management practices are threatening the long-term conservation of a number of animal, fungi, and plant species worldwide. Although unmanaged forests are considered important for biodiversity, forest management continues to affect these vital habitats. We systematically reviewed the scientific literature to gain insight into the effects of forest management abandonment on biodiversity. We calculated log response ratio effect sizes to perform a meta-analysis on species richness between still managed (MAN) and no longer managed (NLM) forests, throughout the world's boreal and temperate forest ecosystems. Our statistical approach included improvements relative to a rigorous treatment of pseudo-replication, an objective choice of taxonomic resolution, and new forms of residual heterogeneity. In our simplest model, plant species richness was significantly lower in NLM than in MAN stands (−14.7 %), while fungi (+10.2 %) and animal (+10.6 %) richness were higher in NLM sites but not significantly (at the 5 % level). Models were improved by adding precipitation, time since abandonment of management (TSA), and their interaction. Effect size estimate for total species richness in NLM forests significantly increased with TSA in wetter climates (+14.3 %), but decreased with TSA in drier climates; fungi richness (+18.1 %) became significantly higher in NLM. These results underline the taxa-dependent responses to management abandonment as well as the slow but real context-dependant recovery capacity of biodiversity after management abandonment. Our findings support the call for further coordinated research to confirm identified patterns, then context-relevant policies aiming to set aside forest zones in production forest systems for conservation purposes.

1. Introduction

Anthropogenic land-use change has substantially altered the structure and functioning of the Earth's ecosystems over time (Vitousek et al., 1997; Findell et al., 2017; Jung et al., 2019). Among the many different human activities, which vary in intensity and effects, forestry is a known driver of biodiversity loss (IPBES, 2019). Despite there being increasing examples of sustainable forest management designed on an ecological paradigm, such as natural disturbance-based forestry (Fenton et al., 2009; Kuuluvainen et al., 2021), which promotes multiple-scale ecological processes, growing evidence suggests that management practices continue to threaten the long-term conservation of a number of

vertebrate (Berg et al., 1994; Cruz et al., 2016), invertebrate (Heliövaara and Väisänen, 1984; Berg et al., 1994), non-lichenized and lichenized fungi (Tomao et al., 2020; Aragón et al., 2010), and plant species (Berg et al., 1994; Hanski, 2011) worldwide. This, in turn, risks jeopardizing global conservation targets (e.g. Aichi target 7 of the Convention on Biological Diversity).

The majority of the world's boreal and temperate forests are subject to forest management. Forests "with no active intervention" represent only 1.8 % of the Europe's total forested area (FOREST EUROPE, 2020), while between 8 and 13 % of the North American Boreal Forest biome is "formally protected" (Wells et al., 2020), and 16 % of Australia's forested area is of the land tenure category "nature conservation reserve" where commercial harvesting is not permitted (Australia SOFR, 2019). This is an illustration that old-growth forests have generally become rare and isolated over time across the planet. In Europe for example, primary forests are now confined to specific ecoregions (e.g. the Carpathians: Uholka-Shyrokyi Luh in Ukraine, and Izvoarele Nerei in Romania) (Sabatini et al., 2018).

Compared to managed forests, unmanaged forest ecosystems are generally considered beneficial for biodiversity (Paillet et al., 2010; Bruun and Heilmann-Clausen, 2021). Since unmanaged forests are prone to small and large natural disturbances—allowing late-successional phases to develop—they tend to have superior structural complexity than managed stands, favouring specific species assemblages (Kozák et al., 2021; McCarthy and Burgman, 1995). Indeed, natural disturbances occurring over a range of spatial and temporal scales likely provide more favourable conditions for different components of biodiversity due to, for example, a greater volume of deadwood (Lassauce et al., 2011; Paillet et al., 2015), presence of very large trees (Paillet et al., 2015; Ali and Wang, 2021), and greater microhabitat presence and diversity (Paillet et al., 2017; Winter and Möller, 2008). Moreover, unmanaged forests may even favour certain reciprocal biotic interactions, for instance, specialist species such as red crossbills benefit from old-growth forests through the enhancement of seed production (Benkman, 1993). Further still, some authors have outlined the importance of meso- and micro-climatic or abiotic soil variables when explaining biodiversity differences between such forests (Halpern and Spies, 1995; Brosofske et al., 1997).

Retaining the structural and compositional diversity of forests not only promotes biodiversity (Lindenmayer et al., 2000), but it may also increase resistance and resilience to climate change effects (Barton and Keeton, 2018; Betts et al., 2018) providing an additional argument for passive forest restoration i.e. management abandonment (Noss, 2001; Krug et al., 2012; Sabatini et al., 2020). Indeed, for some organism groups macroclimatic factors, e.g. precipitation, temperature or seasonality have been shown to be important drivers of richness (Müller et al., 2015; Andrew et al., 2019; Kropik et al., 2021). Hence, it may be likely that the relationship between forest management and species diversity is modified by climatic variations; where drier climates can even be a limiting factor (Ódor et al., 2005) and humid climates a positive one (Kropik et al., 2021). Furthermore, recent studies indicate that old-growth forests can alter the relationship between biological populations and climate (Ellis et al., 2009; Betts et al., 2018) e.g. bird species showing negative effects of summer warming had reduced population declines where old-growth forest was prevalent (Betts et al., 2018). Additionally, epixylic bryophytes diversity was shown to increase in relation to precipitation and deadwood volume (Kropik et al., 2021), an important characteristic of unmanaged forests.

Previous meta-analyses have shown that management generally reduces the diversity of various taxonomic groups. However, existing studies are either restricted to a particular continent e.g. Europe (Paillet et al., 2010), or to a particular taxon and biogeographic region e.g. temperate plants (Duguid and Ashton, 2013). In addition, few meta-analyses have attempted to put explicit emphasis on the role of abandonment, often overlooking the importance of attributing precise definitions to 'unmanaged' (e.g. Chaudhary et al., 2016). We henceforth

adopted a precise definition of unmanaged forests, focusing our attention on 'no longer managed forests' in a passive restoration perspective. In addition, to our knowledge, the interactive effects of forest management and macro-climate variables on species diversity have not been previously assessed, despite the tremendous role forests likely play at attenuating global warming. Furthermore, in many past meta-analyses (e.g. see Paillet et al., 2010) a species-grouping resolution is often the imposed taxonomic level as such, even if it remains open to debate which taxonomic resolution should be used. We therefore adopted a more objective way of choosing the taxonomic resolution though a rigorous model selection process. Additionally, problems associated with pseudo-replication (Hurlbert, 1984) due to within-treatment site replicates may lead to misrepresentative results (Halme et al., 2010; Magurran, 2013; Spake and Doncaster, 2017). This can be problematic in meta-analyses as lower effect-size variance generally obtained for pseudo-replicated sites can give a relatively larger contribution to the meta-estimate (Spake and Doncaster, 2017). We thus propose a novel method, in forest studies at least, for calculating effect sizes by using the number of treatment units (stand-scale) instead of the number of measurement units (plot-scale), as the sample size (N). Further still, methodological improvements included comparing – to our knowledge for the first time in ecology – different forms of residual heterogeneity in meta-analyses to demonstrate that this can also impact the level of significance of estimators.

Accordingly, our overall aim was to transfer consolidated and reliable evidence to forest managers, conservation and restoration ecologists alike, on the potential of management abandonment as a restoration tool for different components of biodiversity in boreal and temperate forests ecosystems. Hence, the specific purposes of the paper were, firstly, to provide an original global-scale meta-analysis focusing on richness and abundance metrics in no longer managed forests (abandoned from former management) compared to managed forests in order to adopt a clearer restoration perspective, while testing to what degree effects may depend on climatic context. And secondly, to propose a renewed robust statistical meta-analysis framework with respect to the treatment of pseudo-replication and an objective choice of taxonomic resolution and forms of model residual heterogeneity.

2. Methods

To evaluate the differences of species richness and abundance between currently managed (MAN) and no longer managed (NLM) forest stands, and the effects of time since management abandonment (TSA) and climatic variables in boreal and temperate forest ecosystems, we followed the Environmental Evidence Guidelines and Standards for Evidence Synthesis in Environmental Management (Pullin et al., 2018).

2.1. Components of the review question

Our primary research question was: what is the effect of forest management abandonment on biodiversity, in terms of species richness and abundance, in the world's boreal and temperate forest ecosystems? Our secondary question was: what is the effect of time since abandonment of management on biodiversity? We also studied whether the answer to these questions varied between taxo-ecological groups or according to climatic conditions. In this study, we refer to NLM forests as forest stands that have not been under management for a minimum of 20 years before the primary study took place but have been managed at some point in time historically. The specific nature of the questions comprised five components (Table 1). Cf. Appendix A for a detailed description of selection methods.

2.2. Literature search and screening of articles

Literature searches were carried out in two publication databases: Scopus and Web Of Science Core collection. A supplementary search for

Table 1
Components of the review question.

Type		Definition
Population (s):	All species groups	This included lichenized and non-lichenized fungi, vascular and non-vascular plants, invertebrates, and vertebrates.
Intervention (s):	Passive restoration: the abandonment/discontinuing of forest management	Historically managed stands, but now no longer managed (NLM). This included stands where abandonment of logging dated back to a minimum of 20 years. Thus, 'no longer managed' did not include primary forests (i.e. never managed forests).
Comparator (s):	Any form of forest management	This was defined as any form of biomass extraction from the MAN stand e.g. thinning, clear felling, selective felling, and any form of tree retention or planting. NB. comparators were synchronic (same time, different site) (i.e. Control-Intervention)
Outcome(s)	Species richness and abundance	All total richness and total abundance indices were retained. Diversity indices (e.g. Shannon index) were also retained if adaptable.
Context(s):	Boreal and temperate forest biomes, worldwide.	These biomes were defined based firstly on the Koppën-Geiger classification method (Beck et al., 2018; Kottek et al., 2006). Secondly, we took into account the Köppen-Trewartha corrections, which reclassify middle latitudes in the northern hemisphere, a more adapted classification for climate types of the contiguous united states (Gardner et al., 2020).

articles was carried out using Google Scholar. The search string combined keywords and synonyms describing population, intervention, comparator and outcomes:

(forest*) AND (species OR richness OR abundance OR diversity) AND (natural* OR semi-natural* OR primary OR primeval OR manag* OR unmanag* OR virgin OR old-growth OR remnant* OR ancient* OR log* OR plantation* OR abandonment OR set-aside).

We undertook a three-stage screening process: firstly titles, then abstracts, then full-texts. We undertook a conservative approach i.e. if the qualifying information at each screening stage was not sufficiently detailed, the title or abstract was retained for screening at the next eligible step. We predefined a process for ensuring consistency between screeners (Frampton et al., 2017; Livoreil et al., 2017). This included pilot tests on a sample of 200 titles before screening titles, and a sample 20 abstracts before screening abstracts. Pilot testing helps ensure agreement between screeners; if agreement is not reached this should lead to a revision of the eligibility criteria (Frampton et al., 2017). Kappa Fleiss scores superior to 0.6 were deemed acceptable (Frampton et al., 2017; Pullin et al., 2018). All disagreements were discussed and resolved before starting each screening stage.

2.3. Critical assessment of studies

A 'critical analysis' phase is central to the procedure of systematic reviews and was carried out to assess both internal validity (risk of bias due to confounding ecological factors) and external validity (relevance of study) of all articles retained after the full-text screening stage (Haddaway et al., 2020). Likewise, authors pilot tested pre-defined criteria on a set of articles to ensure consistency between members of the review team (Frampton et al., 2017). Again, all disagreements were

discussed before appraisal began. The critical appraisal was based on the following criteria:

i. "Forest biome type": we only retained articles located in boreal and temperate biomes, selecting the corresponding Köppen-Geiger (KG) or Köppen-Trewartha (KT) climate zones (Kottek et al., 2006; Beck et al., 2018; Gardner et al., 2020) (cf. Table 1). We assumed that equatorial or tropical forests have very different ecological dynamics and management histories than boreal and temperate forests, which led us to exclude tropical rainforest climates.

ii. "Forest management": we considered any anthropogenic pressure related to direct forest wood resource extraction such as thinning, clear felling, selective felling, and any form of tree planting. MAN forests corresponded to stands where trees had been cut (if information is available, at least 10 trees cut per ha) and exported out of the stand within the last 20 years, whether the exact time since last logging event was given or not. Reciprocally, NLM forests corresponded to stands where no tree had been cut during at least the last 20 years but the stand had been logged previously, whether the exact time since last logging intervention was given or not.

iii. "Site type" and "ancient vs recent forests": authors verified that selected studies compared forest plots on similar soil substrates, and topographic conditions (e.g. if a study compared north-facing NLM and south-facing MAN sites, it was excluded). Also, where there was a strong variation of forest ancientness—referring to the time that has passed since a forest was established independent of past and current management (sensu Cateau et al., 2015)—between MAN and NLM stands, articles in question were excluded.

iv. "Gross successional stages": similarly, we only kept studies when not too dissimilar managed and no longer managed successional phases were compared (e.g. young MAN vs. young NLM, young MAN vs. mid-successional NLM), excluding studies comparing e. g. mature NLM forests and young regeneration phases in MAN stands (i.e. <20 years old) (cf. Appendix A).

"Gross successional stages": similarly, we only kept studies when not too dissimilar managed and no longer managed successional phases were compared (e.g. young MAN vs. young NLM, young MAN vs. mid-successional NLM), excluding studies comparing e.g. mature NLM forests and young regeneration phases in MAN stands (i.e. <20 years old) (cf. Appendix A).

v. "Sampling design": this was assessed in terms of 'spatial segregation' i.e. if NLM stands were in a different and remote region of space than the MAN stands this was considered a confounding factor. If information was given in sufficient detail, we applied a 50 km cut-off i.e. studies were not retained if compared stands were separated by >50 km.

vi. "Spatial replication": if no spatial replicates or only temporal replication on a single plot per treatment, articles were excluded.

vii. Lastly, for an article to be included in the analysis, it had to report summary data (i.e. mean, standard deviation, and sample size) comparing species diversity, or abundance (or both) in MAN vs. NLM stands.

2.4. Data extraction and synthesis

All summary data were extracted from the text, tables, and graphs. We used the R package *metaDigisitise* (Pick et al., 2018) to extract data from graphs. We coded both i) the number of replicated blocks within stands as reported in the study (the plot scale i.e. measurement unit; hereafter denoted as 'Nplot') and ii) the number of replicated stands or treatment units (at the stand scale; hereafter denoted as 'Nstand') (cf. Fig. 1). We applied this method to overcome problems associated with pseudo-replication due to within-treatment site replicates. Thus, we
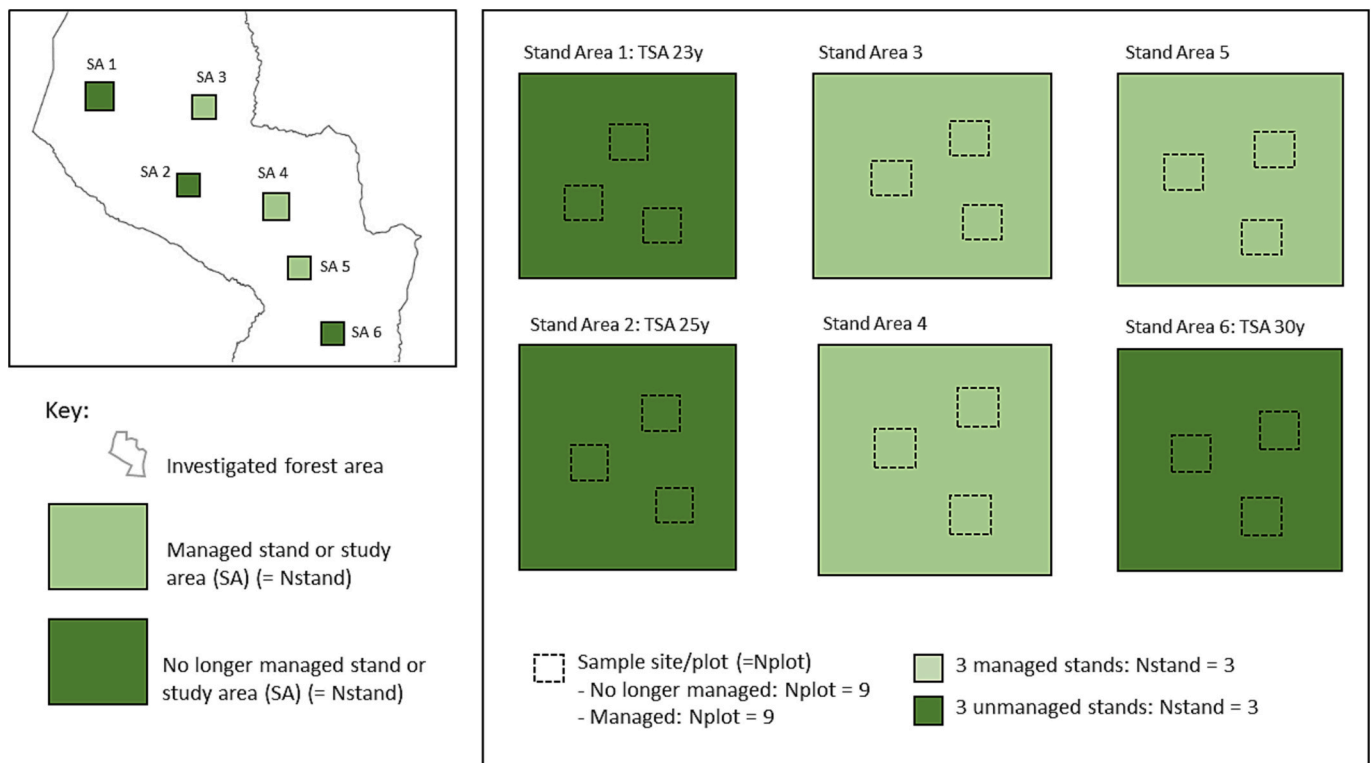
Fig. 1. Schematic representation of the difference between 'Nplot' (forest-plot scale) and 'Nstand' (forest-stand scale).

used the number of treatment units (Nstand), instead of the number of measurement units (Nplot), as the study's sample size (N) for calculating effect sizes.

We allowed multiple entries per article when multiple taxonomic groups were studied, or when several modalities of management were tested. Concerning taxonomic groups, although mean data on subgroups were extracted in addition to data concerning the whole community – e. g. 'total richness of vascular plants' as well as 'richness of plant forest specialists' – only data for the whole community were reported given the low number of cases reported for ecological subgroups (see Table B17). When studies reported a time series e.g. Before-After-Control-Intervention (BACI), we chose the most recent comparison that fulfilled our requirements, translating to a Control-Intervention (CI).

Concerning the classification of species groups, saproxylic beetles i.e. beetle species that depend on deadwood during some part of their life-cycle, were classified separately because they are an important ecological group in forest management studies. This group also comprised bark beetles mentioned as such by the authors. We also defined a broad "saproepixylic" ecological group that combined ecological and taxonomic groups known to depend on diverse forms of deadwood and very large trees, attributes that are generally more abundant in no longer managed forests (Paillet et al., 2015). This group included: saproxylic beetles and bark beetles; invertebrates that are known to be saproxylic or feeding on mainly lignicolous fungi (e.g. *Mycetophilidae*; Fungivorous *Coleoptera*); epixylic, corticolous and lignicolous lichens; lignicolous and saprotrophic fungi; and cavity nesting birds. Bryophytes were not included in our "saproepixylic" ecological group because none of the publications focused solely on corticolous, epixylic or saproxylic bryophytes.

In terms of taxonomic resolution, we compared three classifications: an ad hoc classification similar to that in Paillet et al. (2010), a classification at the level of the taxonomic branch and one at the level of the taxonomic kingdom. For the branch level, we merged the different branches of vascular plants (esp. Angiosperms, different branches of gymnosperms & pteridophyta) and of fungi (i.e. Oomycota,

Zygomycota, Ascomycota, Basidiomycota) since these branches were rarely distinguished in publications. Finally, we assigned each study to the biome in which it was located (either boreal or temperate).

For each individual study, the coordinates (latitude and longitude) were recorded when available. When such data was not available, we used GoogleEarth to extract an estimated location based on sufficiently precise site descriptions provided by authors. Mean annual precipitation and temperature were extracted from WorldClim (www.worldclim.org) (Fick and Hijmans, 2017) in R 4.0.3 (R Core Team, 2020). Finally, we recorded the time since abandonment of management (in years) in managed and no longer managed forests, when available.

2.5. Data treatment and statistical analyses

All the analyses were carried out in R 4.0.3 (R Core Team, 2020) using the package *metafor* for calculation of data (Viechtbauer, 2010) and packages *nimble* and *runMCMCbtadjust* for Bayesian analysis. We used log response ratio effect sizes:

$$lnR = ln\left(\frac{\overline{X}_E}{\overline{X}_C}\right) = ln(\overline{X}_E) - ln(\overline{X}_C) \qquad (1)$$

This effect size gives an estimate of the logarithm of percentage of variation in species richness or abundance between NLM (experimental group, $\overline{X}_E$) and MAN forests (control group, $\overline{X}_C$; see Table 1). It has the advantage of being directly interpretable in terms of magnitude (e.g. Barbier et al., 2009). The variance of the log response ratio is calculated as follows:

$$v = \frac{s_E^2}{n_E \overline{X}_E^2} + \frac{s_C^2}{n_C \overline{X}_C^2} \qquad (2)$$

where s_E and s_C are the standard deviations and n_E and n_C the sample sizes of the experimental and control groups, respectively. Since the same observation can be repeatedly used in different comparisons (e.g. the same data for NLM stands compared with different types of MAN

stands), we modified the variance-covariance used in *metafor* to account for this dependency. For example, when two comparisons shared the same control, their respective variances were given from Eq. (2) but they had non-null covariance: $\frac{s_C^2}{n \, \overline{X}_C^2}$. This yielded what we called the observed variance-covariance matrix, denoted as cov^{obs}.

We first used linear mixed-effect models with Gaussian error distribution to assess the effects of forest management abandonment and other covariates on the log response ratios related to species richness and abundance. We used random-effects models to account for residual heterogeneity in addition to the abovementioned observed variance-covariance matrix cov^{obs}, since ecological data are more subject to uncontrolled variations than data in other scientific fields such as medicine (Pullin and Stewart, 2007; Stewart, 2009; Koricheva et al., 2013). However, we used formulations of this residual heterogeneity that differ from classical ones used in ecology (hereafter called 'restricted additive residual heterogeneity'). Indeed, the classical approach in ecology consists in adding a constant estimated variance to all the variances in cov^{obs}. But it has been recognized in medical meta-analyses (Mawdsley et al., 2017) that another form of model accounting for residual heterogeneity is to multiply the variances by a positive estimated number above one: a model called 'restricted multiplicative residual heterogeneity'. These two models are called restricted because they only affect the variances (i.e. the diagonal of the variance-covariance matrix) and not the covariances. In contrast, unrestricted versions affect the covariances in addition to the variances (hereafter referred to as 'unrestricted additive' and 'unrestricted multiplicative' models of residual heterogeneity). The associated formula for variances are the following, where cov denotes the new variance-covariance matrix: i) $cov_{i,i} = cov_{i,i}^{obs} + sd^2$, in the case of additive residual heterogeneity and ii) $cov_{i,i} = (1 + sd) \, cov_{i,i}^{obs}$, in the case of multiplicative residual heterogeneity, with $sd > 0$. The associated covariances were unchanged compared to cov^{obs} in the case of restricted residual heterogeneity whereas they follow a different formula in the case of unrestricted residual heterogeneity:

$$cov_{i,j} = \sqrt{cov_{i,i} \, cov_{j,j} / \left(cov_{i,i}^{obs} \, cov_{j,j}^{obs}\right)} cov_{i,j}^{obs} \qquad (3)$$

which, in the multiplicative case, simplifies to:

$$cov_{i,j} = (1 + sd) \, cov_{i,j}^{obs} \qquad (4)$$

We added a publication zone-level random effect to take into account that two individual study comparisons issued from the same article zone were potentially more similar than two study comparisons issued from two different publication zones. Then, to ease numerical estimation and model comparisons, this publication random effect was marginalized in the variance-covariance matrix. That is, the random effect disappeared from the linear combination in the mean but was included as an additional term in the variance-covariance matrix. Our final models thus technically resembled Bayesian versions of feasible generalized least squares linear models (Islam et al., 2013; Bai et al., 2021). The final variance-covariance matrix used in the model, cov^{final}, was therefore:

$$cov_{i,j}^{final} = cov_{i,j} + sdPublizone^2 \, \varepsilon_{i,j} \qquad (5)$$

where $\varepsilon_{i,j}$ equals 1 if observations i and j come from the same publication zone, and 0 if otherwise.

Furthermore with the log response ratio, problematic cases can occur when the means of control or treatment groups are near 0, and when the sample size of the standardized mean is small (see Lajeunesse, 2015). As advocated by Lajeunesse (2015), we therefore restricted our main results (Appendix B) to data that fulfilled Eq. (6) from Lajeunesse (2015):

$$\frac{\overline{x}}{SD} \left(\frac{4N^{3/2}}{1 + 4N}\right) \rangle 3 \qquad (6)$$

We however provided results with all the data included in the

analysis (Appendix C) and compared them with our main results.

Given that time since abandonment of management was not available for the entire dataset, we first analysed a "full" dataset including all studies with or without TSA, then added TSA to the models on a data subset (cf. Appendices B to F).

2.5.1. A three-step model-selection approach

For each of our two datasets, we performed three successive series of model comparisons to select the best model in terms of predictive performance.

The first set of models crossed the four different kinds of residual heterogeneity described above with four models for the fixed-effects that targeted different levels of taxonomic resolution moderators. The first model was a null model in which there was only an intercept i.e. no taxonomic information. The three other models included either the taxonomic Branch, Kingdom, or a 'Taxo-Ecological' classification similar to that used in Paillet et al. (2010) (cf. Subsection 2.4). For data where TSA was available, a TSA effect was added to these models. For model comparison, we only kept data where each fixed-effect category had at least nine observations to ensure estimable effects at this taxonomic level and removed data that corresponded to mixed-taxonomic categories for some of these models (e.g. "Vascular Plants + Bryophytes"). Based on a comparison using the Deviance Information Criterion (DIC) (Spiegelhalter et al., 2002), we first selected the best model including a taxonomic level and a residual heterogeneity model. If the best taxonomic resolution model was not the 'Taxo-Ecological' one, some data could subsequently be reinjected since the criterion of at least nine observations per level of fixed effect was now applied to a smaller number of models. In such cases, the model comparison was restarted with more data and less taxonomic models. This, indeed, yielded our best taxonomic residual heterogeneity model.

We then proceeded to a second series of model comparisons that included complexifying the fixed effects of the best model of the first series – keeping the taxonomic resolution and residual heterogeneity model of this best model. This second series of model comparisons compared models based on a series of explanatory variables. For the full dataset, we compared: (i) the null model: only the intercept; (ii) models with one explanatory variable among the taxonomic resolution selected from the first series of model comparisons, the SaproEpixylic character of the group, the biome, the precipitation and temperature; (iii) models with additions of two of the previous explanatory variables; (iv) models with two explanatory variable interactions; and (v) two models with additions of two interactions: the SaproEpixylic character of the group by temperature and precipitation; then the taxonomic groups by temperature and precipitation. For the TSA dataset, we also compared the null model with models including the taxonomic groups, with additions of biome, TSA, precipitation, temperature, as well as interactions of TSA with temperature, precipitation and/or biome (cf. Appendix B). In cases where biome and precipitation and/or temperature were retained in the same model, precipitation and temperature were centred by biome to control for collinearity. Otherwise, all numeric parameters were centred and scaled.

Finally, we undertook a third series of model comparisons, varying the residual heterogeneity model with the best fixed-effect model of the second set of comparisons in cases where it was different from the best model from the first phase. This resulted in our best model for the dataset. The aim of this thorough model comparison approach was to elucidate whether moderators other than the taxonomic groups had a relationship–either in addition or in interaction–with biodiversity differences between NLM and MAN forests.

2.5.2. Applying Bayesian modelling

Given the new models for residual heterogeneity were not available in the R metafor package, we chose to write, estimate and analyse our meta-analyses as Bayesian *Nimble* models. Package *runMCMCbtadjust* allowed us to rigorously control Bayesian convergence (minimum

Gelman Rubin statistic equal to 1.05) and the number of effective values (minimum >4000 and median >6000), ensuring that the outputs were representative samples of the posterior distribution of the Bayesian model. We used DIC to perform model selection since it is a priori applicable in settings where the observations are not independent, which was the case here due to non-null covariances in the variance-covariance matrix. This is not the case for more recent and elaborate techniques (e.g. WAIC in Watanabe, 2012; looIC in Vehtari et al., 2017). Bayesian models had uninformative prior distributions for the fixed effects (a centered Gaussian distribution with standard deviation equal to 1000 for mean parameters and a uniform distribution between 0 and 100 for the two standard deviations). We considered that species richness differed significantly between MAN and NLM forests if the *p*-value (*p*) of the intercept (the parameter associated with treatment/control effect) was inferior to 0.05. We repeated this analysis for both effects of management abandonment and TSA on species richness.

We qualitatively diagnosed best meta-analytic models with classical funnel plots (Sterne and Egger, 2001) in the *metafor* package.

3. Results

3.1. Bibliometric description

After screening of publications and data management (cf. Subsection 2.5), our final dataset comprised 127 individual comparisons on species richness between NLM and MAN forests extracted from 55 articles (cf. Appendix H). This included 79 comparisons in Europe, followed by 25 in Asia, 22 in North America, and one study in Oceania (Fig. 2). In terms of data distribution, plants (vascular plants and bryophytes combined) were the most represented 'Kingdom' (64 comparisons). Fungi (lichenized and non-lichenized combined) were well represented (31 comparisons). Concerning animals (birds and insects), a total of 32 comparisons were retained. The number of comparisons on species richness was almost equal between biomes: 64 in temperate, and 63 in boreal forests (cf. Table 2). Lastly, analyses and results on abundance (42 individual comparisons) are provided in Appendix F.

3.2. Species richness responses to management abandonment

Based on DIC, the best model contained the additive residual heterogeneity (Tables B2 to B5), with taxonomic group at the kingdom level as the explanatory variable:

Table 2
The distribution of the number of comparisons (n = 127, from 55 articles) for species richness of different taxa across biomes for analyses at the 'Kingdom' level.

Taxa classification		Biomes		Total
Kingdom[a]	Ecological	Temperate	Boreal	
Animals	All	9	23	32
	Birds	6	6	12
	Other arthropods[b]	1	10	11
	Carabids	2	0	2
	Saproxylic beetles	0	7	7
Fungi	All	14	17	31
	Non-lichenized fungi	11	8	19
	Lichenized fungi	3	9	12
Plants	All	41	23	64
	Bryophytes	7	2	9
	Vascular plants	34	20	54
	Vascular plants & bryophytes[c]	0	1	1
Total		64	63	127

[a] The analysed taxonomic resolution in models.
[b] "Other" refers to all arthropods other than "carabids" and "saproxylic beetles", which were classed separately because they are important ecological groups in forest management studies.
[c] Where ecological groups were not distinguished in primary studies.

- Plants had significantly lower species richness in NLM forests compared to MAN forests (−14.7 %; Table 3).
- Fungi (+10.2 %) and animal species (+10.6 %) richness were non-significantly (at the 5 % level) higher in NLM forests than in MAN forests (Table 3).

3.3. Species richness responses to time since abandonment of management

We then tested time since abandonment (TSA) in NLM forests (n = 90 study comparisons, from 35 articles), as an explanatory variable where possible. The best model (lowest DIC) comprised taxonomic group at the Kingdom level, TSA, mean precipitation, and the interaction between TSA and precipitation as explanatory variables with an additive residual heterogeneity (Tables B19 to B23). The results resemble the previous model but with important additional information:

- Significantly higher fungi species richness in NLM forests (+18 %), while plant richness remained lower in NLM compared to in MAN forests (−10.7 %), respectively (Table 4; Fig. 3).
- Although mean precipitation and TSA had no significant individual effect, their interaction was statistically significant (Fig. 4A; Table 4) since the differences in species richness between NLM and MAN forests increased with TSA in wetter climates, but decreased with TSA in drier climates (Fig. 4).
- Grand mean models showed that the overall mean effect of management abandonment was not significant (Tables B13, B31 & B32).

3.4. Sensitivity analysis and comparisons of species richness models

The choice of the residual heterogeneity model had some impact on inference. For the full dataset, the fungi intercept was only significant at 5 % for the two models involving multiplicative residual heterogeneity (Tables B10 & B11), but not for the additive versions (Tables B9 & B12). For the TSA dataset, the *p*-value of the Precipitation:TSA interaction varied strongly with the residual heterogeneity model, from a level below 0.02 for the best additive version, to values slightly <0.05 for the restricted additive versions, <0.1 for the multiplicative and >0.1 for the residual multiplicative one (see Tables B27 to B30). If we had only used restricted additive residual heterogeneity, the one used in the *metafor* package, we would have selected the same 'best' model for the full dataset, but we would have selected the model with only the Kingdom fixed-effect for the TSA model (Appendix E). With regards to the Lajeunesse (2015) criterion, had we not applied this rule (Appendix C), we would have still selected models with the same fixed and residual heterogeneity – additive – structures but with slightly different estimates (Tables C6 & C17).

If we had replaced Nstand by Nplot (Appendix D), results would have been completely different: best models would have only included the 'Taxo-Ecological' grouping of species and not Kingdom, both for the full and the TSA datasets (i.e. Kingdom + TSA x Precipitation was no longer the best model) (see Tables D3 & D12).

Finally, funnel plots for both best models did not reveal problems in the data (Figs. B1 & B3). More asymmetry in relation to standard error was detected in Nplot models than in Nstand ones, and when Lajeunesse (2015) criterion was not applied (Figs. C1, C2, D1, D2).

4. Discussion

4.1. Response of species richness to discontinuing management

The results of the current meta-analysis highlight that richness and abundance of species within taxonomic kingdoms respond differently to the abandonment of forest management. Plant richness was significantly lower in NLM forests when compared to forests still under management (mean ± se: −0.1595 ± 0.0432; −14.7 %). When precipitation and TSA were included in the respective models, plant species remained
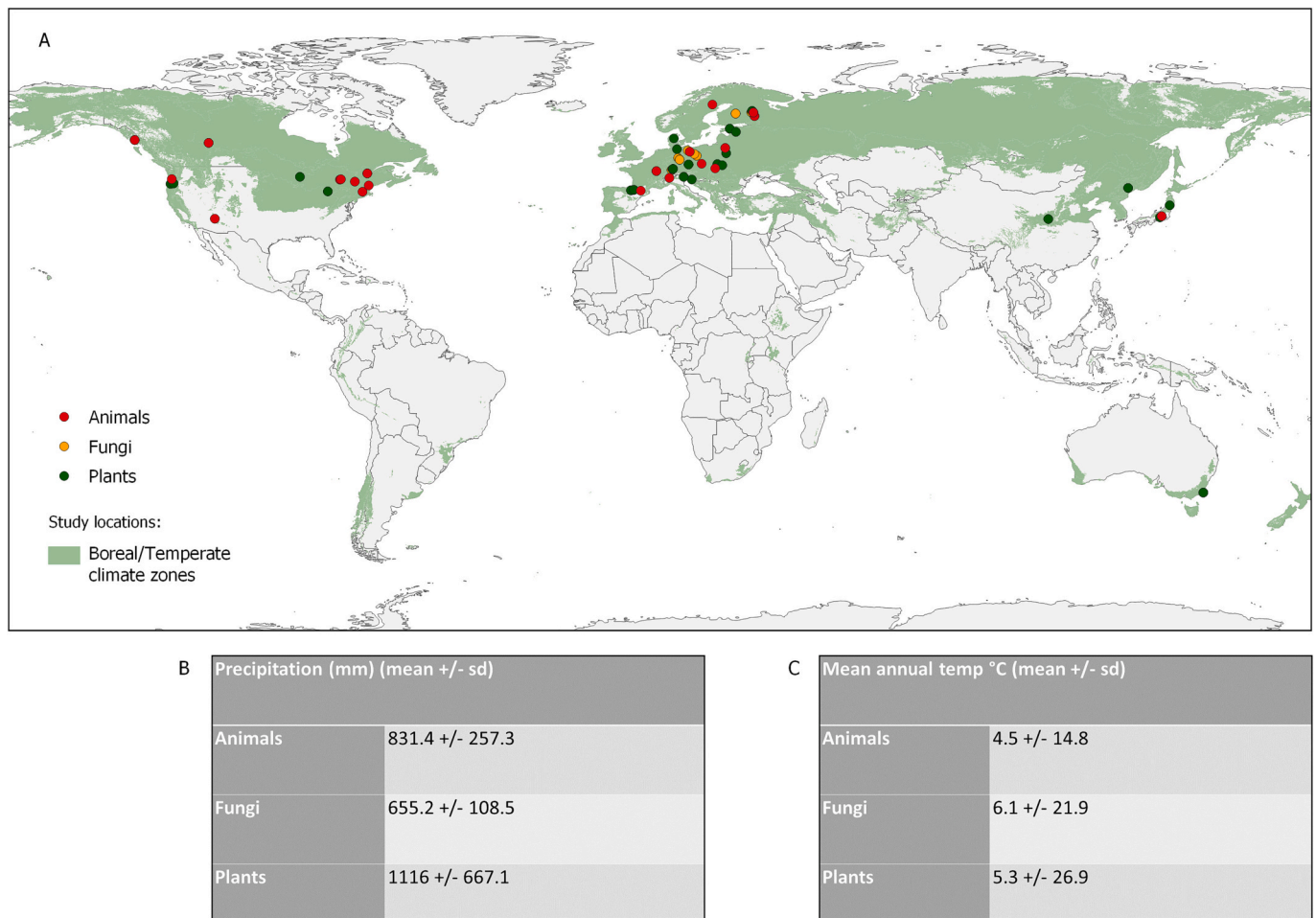
Fig. 2. Geographical locations of included studies (A), mean annual precipitation (mm) (B), and mean annual temperature (°C) data (C) for the three kingdom categories. The extent of the boreal and temperate zones is based on Köppen-Geiger - Peel et al. (2007), and Köppen-Trewartha – Gardner et al. (2020).

Table 3
Results of the best log-response ratio model (with additive residual heterogeneity) for the whole dataset (n = 127 comparisons, from 55 articles), on the effects of forest management abandonment on species richness at the stand-scale in temperate and boreal climatic zones.

	Estimate	SE	CI.lw	CI.up	p	Significance category	% change
Animals	0.1004	0.0554	−0.0067	0.2103	0.0662	(*)–	10.6
Fungi	0.0976	0.0578	−0.0141	0.2125	0.0913	(*)–	10.2
Plants	**−0.1595**	**0.0432**	**−0.2428**	**−0.0723**	**9e−04**	*******	**−14.7**
sd	0.1999	0.0242	0.1556	0.249	NA	NA	NA
sdPublizone	0.0914	0.0483	0.0064	0.1838	NA	NA	NA

Estimate = log response ratio. SE: standard-error of the estimate based on posterior standard deviation. CI.lw and CI.up: lower and upper 95 % credibility intervals. p = critical probability. Notations of significance categories: (*) $p < 0.1$, *$p < 0.05$, **$p < 0.01$, ***$p < 0.001$, ns = non-significant result. (In bold text – significant $p < 0.05$). %: variation between managed and no longer managed forests; a positive value signifies higher richness in no longer managed forests.

statistically more diverse in MAN forests but fungi richness (mean ± se: 0.1664 ± 0.075; 18.1 %)—taxonomic groups dependent on substrates (e.g. tree trunks, deadwood)—became statistically significantly greater in NLM forests, suggesting that responses may be context-dependant. While species abundance appears driven primarily by TSA (cf. Appendix F17).

A number of mechanisms may explain the effects of forest harvesting on forest taxa diversity (Zeller et al., 2023). Concerning fungi taxa, our meta-analysis showed that species richness is significantly higher once logging has been abandoned. Indeed, fungi richness has been shown to be positively related to tree species diversity and deadwood (Lassauce et al., 2011; Tomao et al., 2020), both commonly higher in unmanaged stands (Gazda et al., 2015). With regards to deadwood habitats, larger logs which hold more moisture tend to decay slower than smaller

deadwood favouring the persistence of species groups dependant on substrates (Humphrey et al., 2002). Indeed, fungal communities such as trunk rotters constitute an important group of habitat specialists that depend on such decaying logs (Heilmann-Clausen et al., 2014). But late-decay stage specialist species such as basidiomycetes may equally show preferences for various sizes of well-decayed wood (Heilmann-Clausen et al., 2014), and various stages of decay (Herrmann et al., 2015). Moreover, intensive silvicultural practices are known to reduce the diversity of ectomycorrhizal and wood-inhabiting species (Tomao et al., 2020), whereas late-successional characteristics and stand structural complexity, both of which may be more prevalent in NLM stands (e.g. Humphrey et al., 2002; Paillet et al., 2015), likely improve fungi (lichenized and non-lichenized) species richness (Paillet et al., 2010; Lassauce et al., 2011; Halme et al., 2013; Tomao et al., 2020). Further,

Table 4
Results of the best log-response ratio model for TSA dataset (with additive residual heterogeneity) (n = 90 comparisons, from 35 articles), on the effects of time since forest abandonment (TSA) of management on species richness in temperate and boreal forests.

	Estimate	SE	CI.lw	CI.up	p-Value	Significance category	% change	Mean TSA (±SD)	Mean PRECIP mm (±SD)
Animals	0.0914	0.0786	−0.0607	0.2477	0.2422	ns	9.6	45.1 ± 14.8	831.4 ± 257.3
Fungi	**0.1664**	**0.075**	**0.0215**	**0.3129**	**0.0262**	*	**18.1**	60.8 ± 22	655.2 ± 108.5
Plants	**−0.1138**	**0.0547**	**−0.2193**	**−0.0035**	**0.0442**	*	**−10.8**	53.5 ± 26.9	1116 ± 667.1
Scaled TSA.NLM	−0.0039	0.0419	−0.084	0.0817	0.9131	ns	−0.4	53.8±23.9	/
Scaled Precipitation	0.0679	0.0638	−0.0569	0.1943	0.2876	ns	7	/	927.9±531.8
Scaled TSA.NLM × Scaled Precipitation	**0.1356**	**0.0593**	**0.0211**	**0.2549**	**0.0182**	*	**14.5**	53.8±23.9/	927.9±531.8
sd	0.2032	0.0267	0.1531	0.2576	NA	NA	NA	NA	NA
sdPublizone	0.0962	0.0544	0.0062	0.2071	NA	NA	NA	NA	NA

Estimate = log response ratio. SE: standard-error of the model. CI.lw and CI.up: lower and upper 95 % credibility intervals. p = critical probability. (*) $p < 0.1$, *$p < 0.05$, **$p < 0.01$, ***$p < 0.001$, ns = non-significant result. (In bold text – significant with $p < 0.05$). % variation between managed and no longer managed forests. A positive value means higher richness in no longer managed forest.
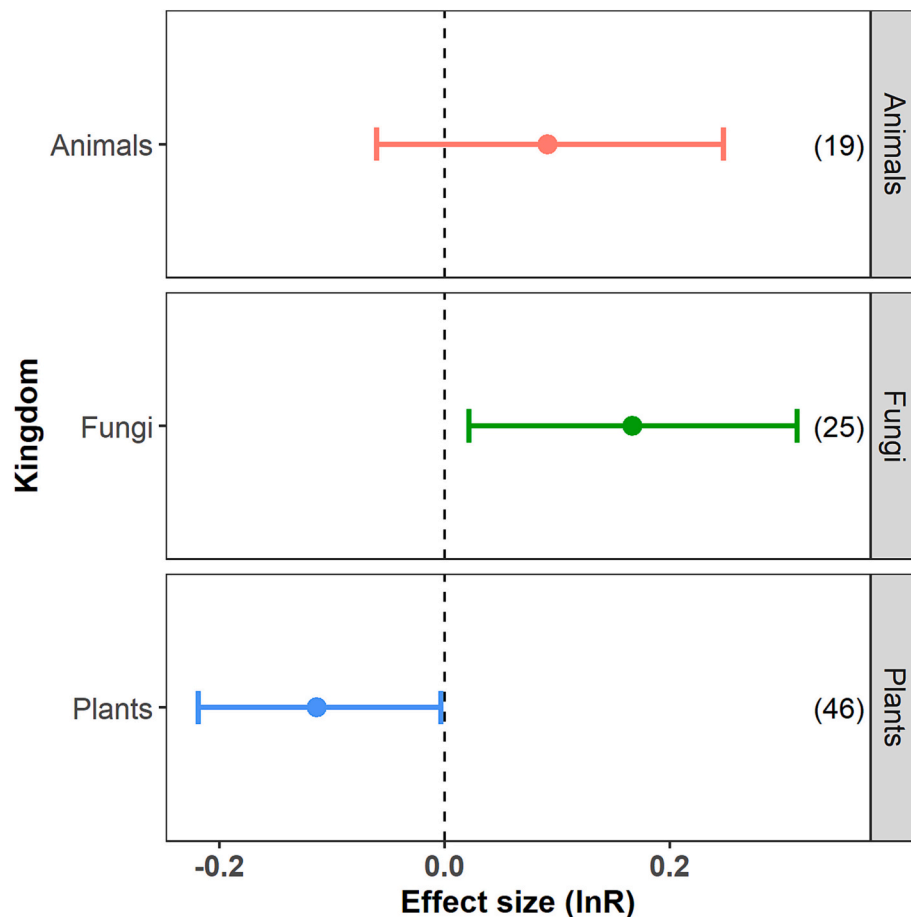

Fig. 3. Comparison of species richness (at the Kingdom level) between NLM and MAN forests (effect size = log response ratio, lnR) from the TSA dataset (Table 4). These represent estimates for the mean values of TSA and precipitation. Bars represent 95 % credibility intervals. A positive value means higher richness in forests where management has been abandoned. Numbers in parentheses signify number of comparisons.

previous studies from Fennoscandia have reported a clear relationship between lack of naturalness and the depletion of fungal communities (e. g. Penttilä et al., 2006; Nordén et al., 2013). Thus, once management has ceased, the dynamics of forest ecosystems should gradually restore back to appropriate conditions, likely aiding the recolonization of species dependent on substrates.

Conversely, species richness of plants was higher in MAN forests. Indeed, certain logging practices (e.g. selection harvesting, retention cuts) induce small-scale disturbances via successive canopy openings that result in increased environmental heterogeneity (Oheimb and

Haerdtle, 2009; Chaudhary et al., 2016), litter removal, and soil disturbance (Orczewska et al., 2019). Moreover, the extraction of trees and successive planting of new stands affect the environmental conditions of the forest floor. Notably, light availability resulting from management-moderated tree composition and age structure can greatly influence plant species richness (Dormann et al., 2020). Therefore, when tree canopies do not dominate the forest site, ground vegetation (herb and shrub layer) can contribute to biomass accumulation (Duguid and Ashton, 2013; Krug, 2019). These factors may particularly favour vascular plants and promote cover and richness of early-successional,

shade-intolerant forest species (Boch et al., 2013; Orczewska et al., 2019). In addition, artificial characteristics such as ditches, and/or logging tracks constitute interesting sources of moderate disturbance (Wei et al., 2015), which favour the availability of resources e.g. light and nutrients, and thus contribute to an enrichment of vascular plants of many ecological groups (Wei et al., 2015, 2016). However, scale may be a driving factor as β-diversity in vascular plants was shown to be higher

in primeval forests (see Kaufmann et al., 2017).

4.2. The role of time since forest management abandonment

While time since abandonment of management appears to drive species abundance (Appendix F), an interaction with precipitation significantly affected the differences in total species richness between
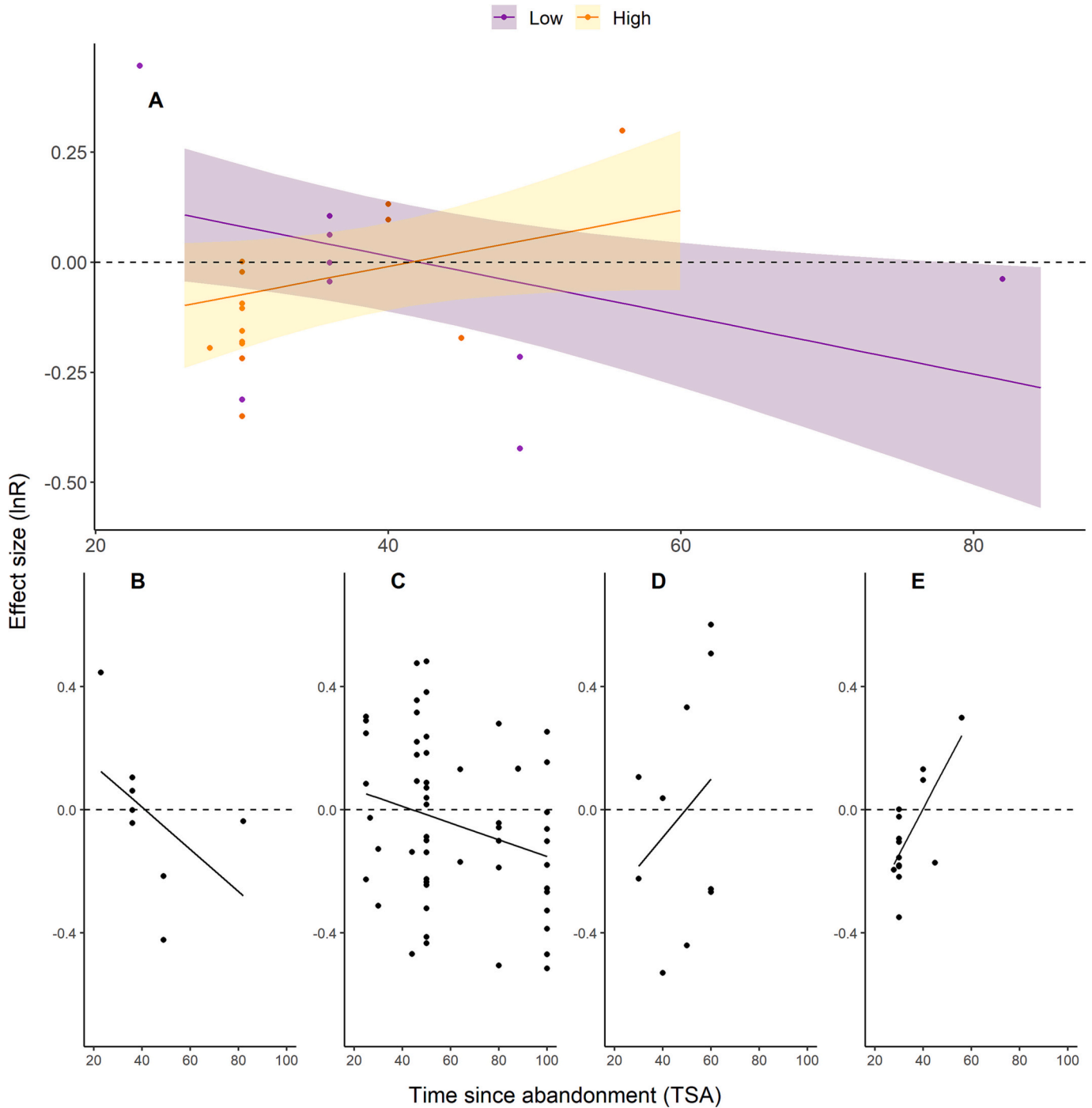

Fig. 4. (A) Representation of the relationship between the difference in species richness between NLM and MAN forests (effect size = log response ratio, ln R) and time since the last harvesting operation in NLM forests depending on precipitation. "Low" precipitation means below the theoretical first quartile (561 mm/year); "High" precipitation is above the theoretical third quartile (1184 mm). A positive value means higher richness in NLM forests. Points correspond to taxonomic residuals of effect sizes (i.e. differences between effect sizes and modelled mean taxonomic levels). (B) Precipitations below the theoretical 25 % quantile: 561 mm/year. (C) Precipitations between the theoretical 25 % and the theoretical median: 561 and 926 mm/year. (D) Precipitations between the theoretical median and the theoretical 75 % quantile: 926 and 1184 mm/year. (E) Precipitations above the theoretical 75 % quantile: 1184 mm/year. Lines of best fit in (B) to (D) are based on a separate linear regression for each panel of residuals vs TSA.

NLM and MAN forests, illustrated by the positive response of effect sizes to TSA in humid climates (e.g. >1184 mm/yr) and the negative response in drier climates (e.g. <561 mm/yr) (Fig. 4A). Thus, in wetter climates, these results support the slow but real recovery of alpha diversity. Further, the results of the best model in Fig. 4A were confirmed by analysing the residuals of weighted differences in species richness between NLM and MAN stands from which the taxonomic Kingdom effects from the best model were removed. Indeed, these residuals showed a strongly negative relationship with TSA in very dry forests (Fig. 4B), a mildly negative relationship in less dry forests (Fig. 4C), a positive relationship in wetter forests (Fig. 4D) and a strongly positive one in the wettest forests (Fig. 4E). This interaction between TSA and precipitation in a meta-analysis is to our knowledge new; it may be explained by at least two mechanisms. First, higher precipitation could imply a greater development of unmanaged-forest characteristics favouring species groups associated with these forests and thus increasing the difference between NLM and MAN stands. For example, while deadwood volume is known to increase with stand age in unmanaged sites (Bujoczek et al., 2021), greater moisture and precipitation may further increase decomposition rate favouring fungi communities (Lustenhouwer et al., 2020). This may permit the rapid expression of all types of decomposition classes, thus favouring saproxylic richness. On the other hand, drier climates may reduce the occurrence of strongly decomposed deadwood, especially if the dominant species have slow annual decomposition rates, e.g. oak (Öder et al., 2021), which is coherent with observations of very few late-decomposition deadwood classes in Mediterranean oak forests (Lombardi et al., 2008). Second, higher precipitation may have important impacts on the natural disturbance of forest stands, increasing the production of deadwood and the opening of at least part of the canopy. Equally, heavy precipitation lengthens periods of high soil moisture, which can affect root anchoring, leading to favourable conditions for wind falls (Mitchell, 2013). In addition, trends towards slower volume loss of deadwood at high precipitation has been revealed (Oettel et al., 2023). Although differences in deadwood volume between NLM and MAN forest are not always statistically different in mean climates, deadwood volume increases from dry sites to wet sites (Bujoczek et al., 2021). This may suggest that if some species depend particularly on substrates, their presence may be favoured in NLM forests in moist climates, explaining the interaction effect. In contrast, drier climates may come with increased risk of fires in the abandoned landscape. Indeed, fire intensity and severity are well correlated to amount of combustible fuels (Dove and Hart, 2017), which may increase in unmanaged sites over time. Severe fire events can reduce the development of late-successional stages and drastically open the canopy which can be detrimental to some taxonomic groups (Dove and Hart, 2017). Finally, it remains to be seen if mechanisms related to canopy cover increase with management cessation and precipitation, and whether precipitation interception (e.g. Barbier et al., 2009) could play a role with regards to this interaction effect.

In the general framework of forest management related biodiversity indicators, our results resemble those of Zilliox and Gosselin (2014) who demonstrate that relationships between indicators and biodiversity are likely to vary according to the ecological context (e.g. with precipitation, with soil acidity, aspect and altitude). These results call for further studies focusing on the ecological context dependence of biodiversity and forest management relationships.

4.3. A case for improved meta-analytical statistical approaches

We used a renewed objective approach – compared to classical meta-analyses – based on model comparison techniques in order to choose the optimal taxonomic resolution in models in terms of predictive ability. Consequently, based on the data at hand, Kingdom resolution was retained in the most parsimonious models. We argue in favour of such an approach rather than subjectively imposing a taxonomic resolution. However, this result does not mean that Kingdom resolution will always

be preferable; with more data, it is likely that more precise resolutions will be favoured. Another improvement was the introduction of four different types of residual heterogeneity structures. The choice of the best structure was also based on DIC. Our sensitivity analyses in Subsection 3.4 indicate that this improvement provided more precise *p*-values of estimated effects in some contexts. The use of the multiplicative residual heterogeneity structure – also known as the weighted least squares method (Mawdsley et al., 2017)– is to our knowledge new in ecology. Although the additive structure was preferred with Nstand models, the multiplicative model is of interest to our field as this method seems to perform better than additive methods in medicine in terms of predictive performance (i.e., Information Criterion such as Akaike's), and significant estimates (Mawdsley et al., 2017; Stanley et al., 2023). We also strongly recommend taking into better account potential pseudo-replication issues in meta-analyses by considering the number of replicated stands (Nstand) as the number of replicates rather than the number of measurement units (Nplot). This choice is in line with Hulbert's (1984) call to ecologists to systematically account for pseudo-replication in the design and interpretation of ecological experiments and observations. This seems yet under-practiced in meta-analyses in ecology. For example, it was not used in previous meta-analyses on a similar subject (e.g. Paillet et al., 2010; Chaudhary et al., 2016). Indeed, Spake and Doncaster (2017) identify this pseudo-replication issue as a challenge for meta-analyses in forest biodiversity research. They advise either i) not to weight, or ii) to weight by "the true sample size of independent replicates", which is what we did through the consideration of the number of replicated stands (Nstand) instead of the number of measurement units (Nplot). The results from both methods in the same conditions in Appendix C (Nstand) and Appendix D (Nplot) are very different in terms of the best taxonomic resolution selected and best model selected. For instance, the Nplot best TSA models did not include the TSA*Precipitation interaction found with Nstand. It is interesting to note that while carabid beetles, which showed strong negative associations with managed forests in Paillet et al. (2010) – who used the Nplot method – showed the inverse result in our best TSA 'Nplot' model (cf. Tables D4 and D13). This sign inversion indeed concerns the taxonomic group that was targeted by Halme et al. (2010) as having marked pseudo-replication issues. This variability in results of models not accounting for pseudo-replication recalls the observation made by Gosselin (2015) that a mere error in one data of a model not accounting for pseudo-replication led to an inversion of signs, with both effects being highly significant. We conclude from these various pieces of evidence that models with numbers of treatment units (Nstand) should be preferred to models with the number of measurement units (Nplot) because this better controls for pseudo-replication issues and should lead to more reproducible results.

4.4. Limits of the review and its meta-analytical approach

One limit of the review was its potential lack of comprehensiveness (e.g. articles written in languages other than English were not included, and use of only two bibliographic databases with a single supplementary search in google scholar), that may have led to missing relevant evidence. Concerning the critical analysis of articles, although we controlled for risk of bias as much as possible, a lack of detail sometimes prevailed in the reporting of important elements such as ancientness, specific site type conditions, and past management histories. We also found it challenging to code information on the spatial structure and the surface area of the sampled forest stands, which may also be important explanatory variables. Our critical analysis did not include criteria on studies controlling for landscape variables or configuration, this may be something to reconsider in futures meta-analyses as the surrounding landscape could influence the forest management effect, especially for mobile groups such as birds (Brotons et al., 2003; Paillet et al., 2010). Finally, another possible limitation is the metric studied, namely alpha diversity. From a practical point of view, it is a simple metric that is used

in many primary studies, but it does not reflect compositional changes (between NLM and MAN forests) nor the variability of species assemblages between plots (Lelli et al., 2019; Schall et al., 2020). And it may not be the most relevant metric in terms of conservation as restoration of specialist species is usually the desired goal, rather than maximising local diversity. A final limitation of our analysis and of the data on which it is based is that few of the data were based on an experimental approach and we did not use a BACI procedure to calculate our meta-analysis metrics.

4.5. Knowledge gaps and clusters

Although the distribution of studies included in our meta-analysis depended on the selection criteria used, a clear knowledge gap concerning several important forest taxa appears to exist in the literature base. There were few reports on arachnids, molluscs, soil fauna diversity, and certain forest insect groups such as syrphid flies and moths already mentioned a decade ago (Paillet et al., 2010). Equally, a paucity of studies on terrestrial and flying mammals, and amphibians is also evident. This could be due, in part, to our choice of metric searched in the literature i.e. richness and abundance. For instance, biomass may be the preferred metric when studying soil fauna. For mammals and herpetofauna, a plausible explanation maybe a lack of studies at the community scale as single-species studies are often favoured. In addition, a lack of studies reporting detailed information on forest site management histories made rigorously testing the effect of TSA difficult (Trentanovi et al., 2023). In a time where systematic reviews are being ever more called for in order to transfer consolidated evidence to practitioners and decision makers alike, we strongly suggest that in future research projects—and to facilitate the extraction of data—authors systematically report information on stand characteristics, habitat types, and historic silvicultural information. This would permit a more accurate evaluation of the effects of forest management abandonment on biodiversity recovery.

5. Conclusion: implications for forest research and conservation policy

Our results first confirm that species groups respond differently to management abandonment, some being more diverse in managed (MAN) forests (e.g. plants) and others in no longer managed (NLM) (e.g. fungi). Within the first 100 years of abandonment, our results may provide an argument in favour of stopping forest management for biodiversity restoration in wetter climates, while highlighting the interest of sustainably managed forests in drier climates. However, while species richness can be estimated for forest sites (alpha diversity), it is challenging to generalise to very large areas (gamma diversity) as differences between NLM and MAN sites may depend on spatial scale. Nevertheless, by documenting the role of TSA for components of terrestrial biodiversity and highlighting the differences in terms of species richness between NLM and MAN forests, our work has implications for future research and policy. First, we call for continued research that would aid in confirming and understanding - in terms of ecological groups, ecological mechanisms - the novel patterns found in the current study. Second, where our results are backed up by further empirical findings they would provide an additional argument for the passive restoration of managed forests, especially through the creation of forest reserves and set asides i.e. by stopping logging in portions of managed forests, on a global scale. In wetter climates especially, conservation priority could be given to species groups whose habitats (e.g. deadwood) are most threatened by management practices. Thus, forest management abandonment may be a very appropriate management choice in wetter climates to buffer the negative effects of direct anthropogenic disturbance in the world's boreal and temperate forests (Sabatini et al., 2018, 2020).

CRediT authorship contribution statement

Joseph Langridge: Conceptualization, Investigation, Methodology, Writing – original draft. **Sylvain Delabye:** Investigation. **Olivier Gilg:** Supervision. **Yoan Paillet:** Conceptualization, Investigation, Writing – original draft, Formal analysis. **Yorick Reyjol:** Conceptualization, Writing – original draft, Validation, Supervision. **Romain Sordello:** Supervision. **Julien Touroult:** Supervision, Funding acquisition. **Frédéric Gosselin:** Conceptualization, Methodology, Writing – original draft, Formal analysis, Validation, Supervision, Funding acquisition.

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

The selected data is provided

Appendices. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.biocon.2023.110296.

References

Ali, A., Wang, L.-Q., 2021. Big-sized trees and forest functioning: current knowledge and future perspectives. Ecol. Indic. 127, 107760. https://doi.org/10.1016/j.ecolind.2021.107760.

Andrew, C., Büntgen, U., Egli, S., Senn-Irlet, B., Grytnes, J.-A., Heilmann-Clausen, J., Boddy, L., Bässler, C., Gange, A.C., Heegaard, E., Høiland, K., Kirk, P.M., Krisai-Greilhüber, I., Kuyper, T.W., Kauserud, H., 2019. Open-source data reveal how collections-based fungal diversity is sensitive to global change. Appl. Plant Sci. 7, e01227 https://doi.org/10.1002/aps3.1227.

Aragón, G., Martínez, I., Izquierdo, P., Belinchón, R., Escudero, A., 2010. Effects of forest management on epiphytic lichen diversity in Mediterranean forests. Appl. Veg. Sci. 13, 183–194. https://doi.org/10.1111/j.1654-109X.2009.01060.x.

Australia SOFR, 2019. Australia's State of the Forests Report 2018 (Report). Australian Bureau of Agricultural and Resource Economics and Sciences, Canberra.

Bai, J., Choi, S.H., Liao, Y., 2021. Feasible generalized least squares for panel data with cross-sectional and serial correlations. Empir. Econ. 60, 309–326. https://doi.org/10.1007/s00181-020-01977-2.

Barbier, S., Chevalier, R., Loussot, P., Bergès, L., Gosselin, F., 2009. Improving biodiversity indicators of sustainable forest management: tree genus abundance rather than tree genus richness and dominance for understory vegetation in French lowland oak hornbeam forests. In: Forest Ecology and Management, IUFRO Conference on Biodiversity in Forest Ecosystems and Landscapes, vol. 258, pp. S176–S186. https://doi.org/10.1016/j.foreco.2009.09.004.

Barton, A.M., Keeton, W.S., 2018. Ecology and Recovery of Eastern Old-growth Forests. Island Press.

Beck, H.E., Zimmermann, N.E., McVicar, T.R., Vergopolan, N., Berg, A., Wood, E.F., 2018. Present and future Köppen-Geiger climate classification maps at 1-km resolution. Sci. Data 5, 180214. https://doi.org/10.1038/sdata.2018.214.

Benkman, C.W., 1993. Logging, conifers, and the conservation of crossbills. Conserv. Biol. 7, 473–479.

Berg, Å., Ehnström, B., Gustafsson, L., Hallingbäck, T., Jonsell, M., Weslien, J., 1994. Threatened plant, animal, and fungus species in Swedish forests: distribution and habitat associations. Conserv. Biol. 8, 718–731. https://doi.org/10.1046/j.1523-1739.1994.08030718.x.

Betts, M.G., Phalan, B., Frey, S.J.K., Rousseau, J.S., Yang, Z., 2018. Old-growth forests buffer climate-sensitive bird populations from warming. Divers. Distrib. 24, 439–447. https://doi.org/10.1111/ddi.12688.

Boch, S., Prati, D., Müller, J., Socher, S., Baumbach, H., Buscot, F., Gockel, S., Hemp, A., Hessenmöller, D., Kalko, E.K.V., Linsenmair, K.E., Pfeiffer, S., Pommer, U., Schöning, I., Schulze, E.D., Seilwinder, C., Weisser, W.W., Wells, K., Fischer, M., 2013. High plant species richness indicates management-related disturbances rather than the conservation status of forests. Basic Appl. Ecol. 496–505. https://doi.org/10.1016/j.baae.2013.06.001.

Brosofske, K.D., Chen, J., Naiman, R.J., Franklin, J.F., 1997. Harvesting effects on microclimatic gradients from small streams to uplands in Western Washington. Ecol. Appl. 7, 1188–1200. https://doi.org/10.1890/1051-0761(1997)007[1188:HEOMGF]2.0.CO;2.

Brotons, L., Mönkkönen, M., Huhta, E., Nikula, A., Rajasärkkä, A., 2003. Effects of landscape structure and forest reserve location on old-growth forest bird species in Northern Finland. Landsc. Ecol. 18, 377–393. https://doi.org/10.1023/A:1026148825138.

Bruun, H.H., Heilmann-Clausen, J., 2021. What is unmanaged forest and how does it sustain biodiversity in landscapes with a long history of intensive forestry? J. Appl. Ecol. 58, 1813–1816. https://doi.org/10.1111/1365-2664.13754.

Bujoczek, L., Bujoczek, M., Zięba, S., 2021. How much, why and where? Deadwood in forest ecosystems: the case of Poland. Ecol. Indic. 121, 107027. https://doi.org/10.1016/j.ecolind.2020.107027.

Cateau, E., Larrieu, L., Vallauri, D., Savoie, J.-M., Touroult, J., Brustel, H., 2015. Ancienneté et maturité : deux qualités complémentaires d'un écosystème forestier. C. R. Biol. 338, 58–73. https://doi.org/10.1016/j.crvi.2014.10.004.

Chaudhary, A., Burivalova, Z., Koh, L.P., Hellweg, S., 2016. Impact of forest management on species richness: global meta-analysis and economic trade-offs. Sci. Rep. 6, 23954. https://doi.org/10.1038/srep23954.

Cruz, J., Sarmento, P., Rydevik, G., Rebelo, H., White, P.C.L., 2016. Bats like vintage: managing exotic eucalypt plantations for bat conservation in a Mediterranean landscape. Anim. Conserv. 19, 53–64. https://doi.org/10.1111/acv.12216.

Dormann, C.F., Bagnara, M., Boch, S., Hinderling, J., Janeiro-Otero, A., Schäfer, D., Schall, P., Hartig, F., 2020. Plant species richness increases with light availability, but not variability, in temperate forests understorey. BMC Ecol. 20, 43. https://doi.org/10.1186/s12898-020-00311-9.

Dove, N.C., Hart, S.C., 2017. Fire reduces fungal species richness and in situ mycorrhizal colonization: a meta-analysis. Fire Ecol. 13, 37–65. https://doi.org/10.4996/fireecology.130237746.

Duguid, M.C., Ashton, M.S., 2013. A meta-analysis of the effect of forest management for timber on understory plant species diversity in temperate forests. For. Ecol. Manag. 303, 81–90. https://doi.org/10.1016/j.foreco.2013.04.009.

Ellis, C.J., Yahr, R., Coppins, B.J., 2009. Local extent of old-growth woodland modifies epiphyte response to climate change. J. Biogeogr. 36, 302–313. https://doi.org/10.1111/j.1365-2699.2008.01989.x.

Fenton, N.J., Simard, M., Bergeron, Y., 2009. Emulating natural disturbances: the role of silviculture in creating even-aged and complex structures in the black spruce boreal forest of eastern North America. J. For. Res. 14, 258–267. https://doi.org/10.1007/s10310-009-0134-8.

Fick, S.E., Hijmans, R.J., 2017. WorldClim 2: new 1-km spatial resolution climate surfaces for global land areas. Int. J. Climatol. 37, 4302–4315. https://doi.org/10.1002/joc.5086.

Findell, K.L., Berg, A., Gentine, P., Krasting, J.P., Lintner, B.R., Malyshev, S., Santanello, J.A., Shevliakova, E., 2017. The impact of anthropogenic land use and land cover change on regional climate extremes. Nat. Commun. 8, 989. https://doi.org/10.1038/s41467-017-01038-w.

FOREST EUROPE, 2020. State of Europe's Forests 2020. URL: https://foresteurope.org/state-europes-forests-2020/. (Accessed 20 July 2021).

Frampton, G.K., Livoreil, B., Petrokofsky, G., 2017. Eligibility screening in evidence synthesis of environmental management topics. Environ. Evid. 6, 27. https://doi.org/10.1186/s13750-017-0102-2.

Gardner, A.S., Maclean, I.M.D., Gaston, K.J., 2020. A new system to classify global climate zones based on plant physiology and using high temporal resolution climate data. J. Biogeogr. 47, 2091–2101. https://doi.org/10.1111/jbi.13927.

Gazda, A., Miścicki, S., Chwistek, K., 2015. Tree species diversity and above-ground biomass of natural temperate forest: montane versus lowland forest. Dendrobiology 73, 3–10. https://doi.org/10.12657/denbio.073.001.

Gosselin, F., 2015. Reevaluating Europe's other debt with improved statistical tools. Biodivers. Conserv. 24, 205–211. https://doi.org/10.1007/s10531-014-0799-y.

Haddaway, N.R., Bethel, A., Dicks, L.V., Koricheva, J., Macura, B., Petrokofsky, G., Pullin, A.S., Savilaakso, S., Stewart, G.B., 2020. Eight problems with literature reviews and how to fix them. Nat. Ecol. Evol. 4, 1582–1589. https://doi.org/10.1038/s41559-020-01295-x.

Halme, P., Toivanen, T., Honkanen, M., Kotiaho, J.S., Mönkkönen, M., Timonen, J., 2010. Flawed meta-analysis of biodiversity effects of forest management. Conserv. Biol. 24, 1154–1156.

Halme, P., Ódor, P., Christensen, M., Piltaver, A., Veerkamp, M., Walleyn, R., Siller, I., Heilmann-Clausen, J., 2013. The effects of habitat degradation on metacommunity structure of wood-inhabiting fungi in European beech forests. Biol. Conserv. 168, 24–30. https://doi.org/10.1016/j.biocon.2013.08.034.

Halpern, C.B., Spies, T.A., 1995. Plant species diversity in natural and managed forests of the Pacific Northwest. Ecol. Appl. 5, 913–934. https://doi.org/10.2307/2269343.

Hanski, I., 2011. Habitat loss, the dynamics of biodiversity, and a perspective on conservation. AMBIO 40, 248–255. https://doi.org/10.1007/s13280-011-0147-3.

Heilmann-Clausen, J., Aude, E., van Dort, K., Christensen, M., Piltaver, A., Veerkamp, M., Walleyn, R., Siller, I., Standovár, T., Òdor, P., 2014. Communities of wood-inhabiting bryophytes and fungi on dead beech logs in Europe – reflecting substrate quality or shaped by climate and forest conditions? J. Biogeogr. 41, 2269–2282. https://doi.org/10.1111/jbi.12388.

Heliövaara, K., Väisänen, R., 1984. Effects of modern forestry on northwestern European forest invertebrates - a synthesis. Acta Forestalia Fenn. 189, 1–32. https://doi.org/10.14214/aff.7636.

Herrmann, S., Kahl, T., Bauhus, J., 2015. Decomposition dynamics of coarse woody debris of three important central European tree species. For. Ecosyst. 2, 27. https://doi.org/10.1186/s40663-015-0052-5.

Humphrey, J.W., Davey, S., Peace, A.J., Ferris, R., Harding, K., 2002. Lichens and bryophyte communities of planted and semi-natural forests in Britain: the influence of site type, stand structure and deadwood. Biol. Conserv. 107, 165–180. https://doi.org/10.1016/S0006-3207(02)00057-5.

Hurlbert, S.H., 1984. Pseudoreplication and the design of ecological field experiments. Ecol. Monogr. 54, 187–211. https://doi.org/10.2307/1942661.

IPBES, 2019. Summary for policymakers of the global assessment report on biodiversity and ecosystem services. Zenodo. https://doi.org/10.5281/zenodo.3553579.

Islam, Md.E., Grote, U., Rayhan, Md.I., 2013. Income vulnerability of rural households in Bangladesh: a comparison between Bayesian and classical methods. J. Stat. Comput. Simul. 83, 1179–1187. https://doi.org/10.1080/00949655.2012.656310.

Jung, M., Rowhani, P., Scharlemann, J.P.W., 2019. Impacts of past abrupt land change on local biodiversity globally. Nat. Commun. 10, 5474. https://doi.org/10.1038/s41467-019-13452-3.

Kaufmann, S., Hauck, M., Leuschner, C., 2017. Comparing the plant diversity of paired beech primeval and production forests: management reduces cryptogam, but not vascular plant species richness. For. Ecol. Manag. 400, 58–67. https://doi.org/10.1016/j.foreco.2017.05.043.

Koricheva, J., Gurevitch, J., Mengersen, K., 2013. Handbook of Meta-analysis in Ecology and Evolution, Handbook of Meta-analysis in Ecology and Evolution. Princeton University Press.

Kottek, M., Grieser, J., Beck, C., Rudolf, B., Rubel, F., 2006. World map of the Köppen-Geiger climate classification updated. Meteorol. Z. 259–263. https://doi.org/10.1127/0941-2948/2006/0130.

Kozák, D., Svitok, M., Wiezik, M., Mikoláš, M., Thorn, S., Buechling, A., Hofmeister, J., Matula, R., Trotsiuk, V., Bače, R., Begović, K., Čada, V., Dušátko, M., Frankovič, M., Horák, J., Janda, P., Kameniar, O., Nagel, T.A., Pettit, J.L., Pettit, J.M., Synek, M., Wieziková, A., Svoboda, M., 2021. Historical disturbances determine current taxonomic, functional and phylogenetic diversity of saproxylic beetle communities in temperate primary forests. Ecosystems 24, 37–55. https://doi.org/10.1007/s10021-020-00502-x.

Kropik, M., Zechmeister, H.G., Moser, D., Bernhardt, K.G., Dullinger, S., 2021. Deadwood volumes matter in epixylic bryophyte conservation, but precipitation limits the establishment of substrate-specific communities. For. Ecol. Manag. 493, 119285. https://doi.org/10.1016/j.foreco.2021.119285.

Krug, J.H.A., 2019. How can forest management increase biomass accumulation and CO_2 sequestration? A case study on beech forests in Hesse, Germany. Carbon Balance Manag. 14, 17. https://doi.org/10.1186/s13021-019-0132-x.

Krug, J., Koehl, M., Kownatzki, D., 2012. Revaluing unmanaged forests for climate change mitigation. Carbon Balance Manag. 7, 11. https://doi.org/10.1186/1750-0680-7-11.

Kuuluvainen, T., Angelstam, P., Frelich, L., Jõgiste, K., Koivula, M., Kubota, Y., Lafleur, B., Macdonald, E., 2021. Natural disturbance-based forest management: moving beyond retention and continuous-cover forestry. Front. For. Glob. Change 4. https://doi.org/10.3389/ffgc.2021.629020.

Lajeunesse, M.J., 2015. Bias and correction for the log response ratio in ecological meta-analysis. Ecology 96, 2056–2063. https://doi.org/10.1890/14-2402.1.

Lassauce, A., Paillet, Y., Jactel, H., Bouget, C., 2011. Deadwood as a surrogate for forest biodiversity: meta-analysis of correlations between deadwood volume and species richness of saproxylic organisms. Ecol. Indic. 11, 1027–1039. https://doi.org/10.1016/j.ecolind.2011.02.004.

Lelli, C., Bruun, H.H., Chiarucci, A., Donati, D., Frascaroli, F., Fritz, Ö., Goldberg, I., Nascimbene, J., Tøttrup, A.P., Rahbek, C., Heilmann-Clausen, J., 2019. Biodiversity response to forest structure and management: comparing species richness, conservation relevant species and functional diversity as metrics in forest conservation. For. Ecol. Manag. 432, 707–717. https://doi.org/10.1016/j.foreco.2018.09.057.

Lindenmayer, D.B., Margules, C.R., Botkin, D.B., 2000. Indicators of biodiversity for ecologically sustainable forest management. Conserv. Biol. 14, 941–950. https://doi.org/10.1046/j.1523-1739.2000.98533.x.

Livoreil, B., Glanville, J., Haddaway, N.R., Bayliss, H., Bethel, A., de Lachapelle, F.F., Robalino, S., Savilaakso, S., Zhou, W., Petrokofsky, G., Frampton, G., 2017. Systematic searching for environmental evidence using multiple tools and sources. Environ. Evid. 6, 23. https://doi.org/10.1186/s13750-017-0099-6.

Lombardi, F., Lasserre, B., Tognetti, R., Marchetti, M., 2008. Deadwood in relation to stand management and forest type in Central Apennines (Molise, Italy). Ecosystems 11, 882–894. https://doi.org/10.1007/s10021-008-9167-7.

Lustenhouwer, N., Maynard, D.S., Bradford, M.A., Lindner, D.L., Oberle, B., Zanne, A.E., Crowther, T.W., 2020. A trait-based understanding of wood decomposition by fungi. Proc. Natl. Acad. Sci. 117, 11551–11558. https://doi.org/10.1073/pnas.1909166117.

Magurran, A.E., 2013. Measuring Biological Diversity. John Wiley & Sons.

Mawdsley, D., Higgins, J.P.T., Sutton, A.J., Abrams, K.R., 2017. Accounting for heterogeneity in meta-analysis using a multiplicative model—an empirical study. Res. Synth. Methods 8, 43–52. https://doi.org/10.1002/jrsm.1216.

McCarthy, M.A., Burgman, M.A., 1995. Coping with uncertainty in forest wildlife planning. For. Ecol. Manag. 74, 23–36. https://doi.org/10.1016/0378-1127(94)03523-Y.

Mitchell, S.J., 2013. Wind as a natural disturbance agent in forests: a synthesis. Forestry 86, 147–157. https://doi.org/10.1093/forestry/cps058.

Müller, J., Brustel, H., Brin, A., Bussler, H., Bouget, C., Obermaier, E., Heidinger, I.M.M., Lachat, T., Förster, B., Horak, J., Procházka, J., Köhler, F., Larrieu, L., Bense, U., Isacsson, G., Zapponi, L., Gossner, M.M., 2015. Increasing temperature may compensate for lower amounts of dead wood in driving richness of saproxylic beetles. Ecography 38, 499–509. https://doi.org/10.1111/ecog.00908.

Nordén, J., Penttilä, R., Siitonen, J., Tomppo, E., Ovaskainen, O., 2013. Specialist species of wood-inhabiting fungi struggle while generalists thrive in fragmented boreal forests. J. Ecol. 101, 701–712. https://doi.org/10.1111/1365-2745.12085.

Noss, R.F., 2001. Beyond Kyoto: forest management in a time of rapid climate change. Conserv. Biol. 15, 578–590. https://doi.org/10.1046/j.1523-1739.2001.015003578.x.

Öder, V., Petritan, A.M., Schellenberg, J., Bergmeier, E., Walentowski, H., 2021. Patterns and drivers of deadwood quantity and variation in mid-latitude deciduous forests. For. Ecol. Manag. 487, 118977. https://doi.org/10.1016/j.foreco.2021.118977.

Ódor, P., van Dort, K., Aude, E., Heilmann-Clausen, J., Christensen, M., 2005. Diversity and composition of dead wood inhabiting bryophyte communities in European beech forests. Boletín de la Sociedad Española de Briología (26–27), 85–102. ISSN 1132-8029. (26).

Oettel, J., Zolles, A., Gschwantner, T., Lapin, K., Kindermann, G., Schweinzer, K.-M., Gossner, M.M., Essl, F., 2023. Dynamics of standing deadwood in Austrian forests under varying forest management and climatic conditions. J. Appl. Ecol. 60, 696–713. https://doi.org/10.1111/1365-2664.14359.

Oheimb, G., Haerdtle, W., 2009. Selection harvest in temperate deciduous forests: impact on herb layer richness and composition. Biodivers. Conserv. 18, 271–287. https://doi.org/10.1007/s10531-008-9475-4.

Orczewska, A., Czortek, P., Jaroszewicz, B., 2019. The impact of salvage logging on herb layer species composition and plant community recovery in Białowieża Forest. Biodivers. Conserv. 28, 3407–3428. https://doi.org/10.1007/s10531-019-01795-8.

Paillet, Y., Bergès, L., Hjältén, J., Ódor, P., Avon, C., Bernhardt-Römermann, M., Bijlsma, R.J., de Bruyn, L., Fuhr, M., Grandin, U., Kanka, R., Lundin, L., Luque, S., Magura, T., Matesanz, S., Mészáros, I., Sebastià, M.T., Schmidt, W., Standovár, T., Tóthmérész, B., Uotila, A., Valladares, F., Vellak, K., Virtanen, R., 2010. Biodiversity differences between managed and unmanaged forests: meta-analysis of species richness in Europe. Conserv. Biol. 24, 101–112. https://doi.org/10.1111/j.1523-1739.2009.01399.x.

Paillet, Y., Pernot, C., Boulanger, V., Debaive, N., Fuhr, M., Gilg, O., Gosselin, F., 2015. Quantifying the recovery of old-growth attributes in forest reserves: a first reference for France. For. Ecol. Manag. 346, 51–64. https://doi.org/10.1016/j.foreco.2015.02.037.

Paillet, Y., Archaux, F., Boulanger, V., Debaive, N., Fuhr, M., Gilg, O., Gosselin, F., Guilbert, E., 2017. Snags and large trees drive higher tree microhabitat densities in strict forest reserves. For. Ecol. Manag. 389, 176–186. https://doi.org/10.1016/j.foreco.2016.12.014.

Peel, M.C., Finlayson, B.L., McMahon, T.A., 2007. Updated world map of the Köppen-Geiger climate classification. Hydrol. Earth Syst. Sci. 11, 1633–1644. https://doi.org/10.5194/hess-11-1633-2007.

Penttilä, R., Lindgren, M., Miettinen, O., Rita, H., Hanski, I., 2006. Consequences of forest fragmentation for polyporous fungi at two spatial scales. Oikos 114, 225–240. https://doi.org/10.1111/j.2006.0030-1299.14349.x.

Pick, J.L., Nakagawa, S., Noble, D.W.A., 2018. Reproducible, Flexible and High Throughput Data Extraction From Primary Literature: The metaDigitise R Package 22.

Pullin, A., Stewart, G., 2007. Guidelines for systematic review in environmental management. Conserv. Biol. 20, 1647–1656. https://doi.org/10.1111/j.1523-1739.2006.00485.x.

Pullin, A., Frampton, G., Livoreil, B., Petrokofsky, G., 2018. Collaboration for environmental evidence. In: Guidelines and Standards for Evidence synthesis in Environmental Management. Version 5.0.

R Core Team, 2020. R: A language and environment for statistical computing [WWW Document]. URL. https://www.R-project.org/. (Accessed 23 April 2021).

Sabatini, F.M., Burrascano, S., Keeton, W.S., Levers, C., Lindner, M., Pötzschner, F., Verkerk, P.J., Bauhus, J., Buchwald, E., Chaskovsky, O., Debaive, N., Horváth, F.,

Garbarino, M., Grigoriadis, N., Lombardi, F., Duarte, I.M., Meyer, P., Midteng, R., Mikac, S., Mikoláš, M., Motta, R., Mozgeris, G., Nunes, L., Panayotov, M., Ódor, P., Ruete, A., Simovski, B., Stillhard, J., Svoboda, M., Szwagrzyk, J., Tikkanen, O.-P., Volosyanchuk, R., Vrska, T., Zlatanov, T., Kuemmerle, T., 2018. Where are Europe's last primary forests? Divers. Distrib. 24, 1426–1439. https://doi.org/10.1111/ddi.12778.

Sabatini, F.M., Keeton, W.S., Lindner, M., Svoboda, M., Verkerk, P.J., Bauhus, J., Bruelheide, H., Burrascano, S., Debaive, N., Duarte, I., Garbarino, M., Grigoriadis, N., Lombardi, F., Mikoláš, M., Meyer, P., Motta, R., Mozgeris, G., Nunes, L., Ódor, P., Panayotov, M., Ruete, A., Simovski, B., Stillhard, J., Svensson, J., Szwagrzyk, J., Tikkanen, O.-P., Vandekerkhove, K., Volosyanchuk, R., Vrska, T., Zlatanov, T., Kuemmerle, T., 2020. Protection gaps and restoration opportunities for primary forests in Europe. Divers. Distrib. 26, 1646–1662. https://doi.org/10.1111/ddi.13158.

Schall, P., Heinrichs, S., Ammer, C., Ayasse, M., Boch, S., Buscot, F., Fischer, M., Goldmann, K., Overmann, J., Schulze, E.-D., Sikorski, J., Weisser, W.W., Wubet, T., Gossner, M.M., 2020. Can multi-taxa diversity in European beech forest landscapes be increased by combining different management systems? J. Appl. Ecol. 57, 1363–1375. https://doi.org/10.1111/1365-2664.13635.

Spake, R., Doncaster, C.P., 2017. Use of meta-analysis in forest biodiversity research: key challenges and considerations. For. Ecol. Manag. 400, 429–437. https://doi.org/10.1016/j.foreco.2017.05.059.

Spiegelhalter, D.J., Best, N.G., Carlin, B.P., Van Der Linde, A., 2002. Bayesian measures of model complexity and fit. J. R. Stat. Soc. B 64, 583–639.

Stanley, T.D., Ioannidis, J.P.A., Maier, M., Doucouliagos, H., Otte, W.M., Bartoš, F., 2023. Unrestricted weighted least squares represent medical research better than random effects in 67,308 Cochrane meta-analyses. J. Clin. Epidemiol. 157, 53–58. https://doi.org/10.1016/j.jclinepi.2023.03.004.

Sterne, J.A., Egger, M., 2001. Funnel plots for detecting bias in meta-analysis: guidelines on choice of axis. J. Clin. Epidemiol. 54, 1046–1055. https://doi.org/10.1016/s0895-4356(01)00377-8.

Stewart, G., 2009. Meta-analysis in applied ecology. Biol. Lett. 6, 78–81. https://doi.org/10.1098/rsbl.2009.0546.

Tomao, A., Antonio Bonet, J., Castaño, C., de Miguel, S., 2020. How does forest management affect fungal diversity and community composition? Current knowledge and future perspectives for the conservation of forest fungi. For. Ecol. Manag. 457, 117678. https://doi.org/10.1016/j.foreco.2019.117678.

Trentanovi, G., Campagnaro, T., Sitzia, T., Chianucci, F., Vacchiano, G., Ammer, C., Ciach, M., Nagel, T.A., del Río, M., Paillet, Y., Munzi, S., Vandekerkhove, K., Bravo-Oviedo, A., Cutini, A., D'Andrea, E., De Smedt, P., Doerfler, I., Fotakis, D., Heilmann-Clausen, J., Hofmeister, J., Hošek, J., Janssen, P., Kepfer-Rojas, S., Korboulewsky, N., Kovács, B., Kozák, D., Lachat, T., Mårell, A., Matula, R., Mikoláš, M., Nordén, B., Ódor, P., Perović, M., Pötzelsberger, E., Schall, P., Svoboda, M., Tinya, F., Ujházyová, A., Burrascano, S., 2023. Words apart: standardizing forestry terms and definitions across European biodiversity studies. For. Ecosyst. 10, 100128. https://doi.org/10.1016/j.fecs.2023.100128.

Vehtari, A., Gelman, A., Gabry, J., 2017. Practical Bayesian model evaluation using leave-one-out cross-validation and WAIC. Stat. Comput. 27, 1413–1432. https://doi.org/10.1007/s11222-016-9696-4.

Viechtbauer, W., 2010. Conducting meta-analyses in R with the metafor package. J. Stat. Softw. 36, 1–48. https://doi.org/10.18637/jss.v036.i03.

Vitousek, P.M., Mooney, H.A., Lubchenco, J., Melillo, J.M., 1997. Human domination of Earth's ecosystems. Science 277, 494–499. https://doi.org/10.1126/science.277.5325.494.

Watanabe, S., 2012. A widely applicable Bayesian information criterion. J. Mach. Learn. Res. 14.

Wei, L., Villemey, A., Hulin, F., Bilger, I., Yann, D., Chevalier, R., Archaux, F., Gosselin, F., 2015. Plant diversity on skid trails in oak high forests: a matter of disturbance, micro-environmental conditions or forest age? For. Ecol. Manag. 338, 20–31. https://doi.org/10.1016/j.foreco.2014.11.018.

Wei, L., Hulin, F., Chevalier, R., Archaux, F., Gosselin, F., 2016. Is plant diversity on tractor trails more influenced by disturbance than by soil characteristics? For. Ecol. Manag. 379, 173–184. https://doi.org/10.1016/j.foreco.2016.08.020.

Wells, J.V., Dawson, N., Culver, N., Reid, F.A., Morgan Siegers, S., 2020. The state of conservation in North America's boreal forest: issues and opportunities. Front. For. Glob. Change 3, 90. https://doi.org/10.3389/ffgc.2020.00090.

Winter, S., Möller, G.C., 2008. Microhabitats in lowland beech forests as monitoring tool for nature conservation. For. Ecol. Manag. 255, 1251–1261. https://doi.org/10.1016/j.foreco.2007.10.029.

Zeller, L., Förster, A., Keye, C., Meyer, P., Roschak, C., Ammer, C., 2023. What does literature tell us about the relationship between forest structural attributes and species richness in temperate forests? – a review. Ecol. Indic. 153, 110383. https://doi.org/10.1016/j.ecolind.2023.110383.

Zilliox, C., Gosselin, F., 2014. Tree species diversity and abundance as indicators of understory diversity in French mountain forests: variations of the relationship in geographical and ecological space. For. Ecol. Manag. 321, 105–116. https://doi.org/10.1016/j.foreco.2013.07.049.