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Authors: Yoan Paillet[1,2], Laurent Bergès[1,*], Joakim Hjältén[3], Péter Ódor[4], Catherine Avon[1], Markus Bernhardt-Römermann[5], Rienk-Jan Bijlsma[6], Luc De Bruyn[7,8], Marc Fuhr[2], Ulf Grandin[9], Robert Kanka[10], Lars Lundin[9], Sandra Luque[2], Tibor Magura[11], Silvia Matesanz[12], Ilona Mészáros[13], M.-Teresa Sebastià[14,15], Wolfgang Schmidt[5], Tibor Standovár[4], Béla Tóthmérész[16], Anneli Uotila[17], Fernando Valladares[12], Kai Vellak[18], Risto Virtanen[19]

*corresponding author, mailto: Laurent.Berges@cemagref.fr

[1] Cemagref, UR EFNO, Domaine des Barres, F-45290 Nogent-sur-Vernisson, France

[2] Cemagref, UR EMGR, 2 rue de la Papeterie BP 76, F-38402 Saint-Martin-d'Hères, France

[3] Department of Wildlife, Fish and Environmental Science, Swedish University of Agricultural Sciences, SE-901 83 Umeå, Sweden

[4] Department of Plant Taxonomy and Ecology, Eötvös University, Pázmány P. stny. 1/C., H-1117 Budapest, Hungary

[5] Department Silviculture and Forest Ecology of the Temperate Zones, Georg-August-University Göttingen, Büsgenweg 1, D-37077 Göttingen, Germany

[6] Alterra Wageningen UR, Centre for Ecosystem Studies, P.O. Box 47, NL-6700 AA Wageningen, The Netherlands

[7] Research Institute for Nature and Forest, Kliniekstraat 25, B-1070 Brussels, Belgium

[8] Evolutionary Ecology, Department of Biology, University of Antwerp, Groenenborgerlaan 171, B-2020 Antwerpen, Belgium

[9] Swedish Univ Agr Sci, Department of Aquatic Sciences and Assessment, Box 7050, SE-75007 Uppsala, Sweden

[10] Institute of Landscape Ecology, Slovak Academy of Sciences, Stefanikova Str. 3, SK-814 99 Bratislava, Slovakia

[11] Hortobágy National Park Directorate, P.O. Box 216, H-4002 Debrecen, Hungary

[12] Instituto de Recursos Naturales, CSIC IRN-CCMA-CSIC, Serrano 115, E-28006 Madrid, Spain

[13] Department of Botany, University of Debrecen, P.O. Box 71, H-4010 Debrecen, Hungary

[14] Forest Technology Centre of Catalonia, Pujada del Seminari s/n, E-25280 Solsona, Spain

[15] Agronomical Engineering School, University of Lleida, Av. Rovira Roure 191, E-25198 Lleida, Spain
[16] Ecological Institute, Debrecen University, P.O. Box 71, H-4010 Debrecen, Hungary
[17] Faculty of Forestry, University of Joensuu, P.O. Box 111, FIN-80101 Joensuu, Finland
[18] Institute of Ecology and Earth Sciences, University of Tartu, Lai Str., 40 Tartu EE-51005, Estonia
[19] Department of Biology, University of Oulu, P.O. Box 3000, FIN-90014 Oulu, Finland

Abstract (293 words)

Past and present pressures on forest resources have led to a drastic decrease in the surface area of unmanaged forests in Europe. Changes in forest structure, composition and dynamics inevitably lead to changes in the biodiversity of forest-dwelling species. However, the possible biodiversity gains and losses due to forest management, *i.e.* anthropogenic pressures related to direct forest resource use, have never been assessed at a pan-European scale. We used meta-analysis to review 49 published papers containing 120 individual comparisons of species richness between unmanaged and managed forests throughout Europe. We explored the response of different taxonomic groups and the variability of their response with respect to time since abandonment and type of forest management.

Species richness was slightly higher in unmanaged than in managed forests. Species dependent on forest cover continuity, deadwood and large trees – bryophytes, lichens, fungi and saproxylic beetles – and carabids were negatively affected by forest management. In contrast, vascular plant species were favored. The response for birds was heterogeneous and probably depended more on factors such as landscape patterns. The global difference in species richness between unmanaged and managed forests increased with time since abandonment and indicated a gradual recovery of biodiversity. Plantations with tree species change had the stronger effect on species richness, but the effects of different types of management on taxa could not be assessed in a robust way due to low numbers of replications in the forest management classes. In conclusion, our results show that some taxa are more affected by forestry than others, but we also highlight the need for research into poorly-studied species groups in Europe or specific locations. Our meta-analysis supports the need for a coordinated European research network to study and monitor the biodiversity of different taxa in managed and unmanaged forests.

Introduction

Almost all Europe's native forests have been altered by management of ranging intensity (Vanbergen et al. 2005). Natural forests currently represent less than 1% of the European forest area, against 13% on the west coast of the United States and 40-52% in Canada (Heywood & Watson 1995; Parviainen et al. 2000). Species diversity is increasingly considered key to ecosystem functioning (Scherer-Lorenzen et al. 2005) and recent international commitments have highlighted the need to halt biodiversity loss and promote sustainable management (Parviainen et al. 2007). However, timber-oriented forest management still threatens the survival of many species that depend on natural forest habitats (Bengtsson et al. 2000).

Accordingly, natural forests are considered to be the reference state for sustainable forest management (Angelstam 1998; Angermeier 2000; Wesolowski 2005). In unmanaged forests, occasional large-scale disturbances and frequent small-scale disturbances allow late-successional phases to develop, resulting in a fine-grained mosaic of different developmental phases (Bengtsson et al. 2000). Thus, unmanaged forests display typical features such as large amounts of deadwood and decaying trees, old and large trees, and pits and mounds around root plates (Hunter 1999; Peterken 1996; Spies & Turner 1999). Silvicultural practices throughout Europe have deeply modified the natural disturbance regime, sometimes for several centuries. Managed forest landscapes are currently characterized by frequent disturbances with low variability in disturbance size, and display more homogeneous tree composition, vertical stratification, age structure and successional dynamics while lacking senescent phases (Commarmot et al. 2005; Kuuluvainen et al. 1996).

However, there is still debate over the global effect of forest management on biodiversity (Siitonen 2001). At the local scale, unmanaged forests are generally said to be species richer than managed forests (Okland et al. 2003). However, some studies have failed to confirm this result for certain taxa such as vascular plants, birds and soil invertebrates (Bobiec 1998; Graae & Heskjaer 1997), while others have even found a positive effect of management on the total species richness of vascular plants (Schmidt 2005), beetles (Vaisanen et al. 1993) and carabids (Desender et al. 1999). The scientific literature has therefore failed to support this idea due to conflicting results and the apparently idiosyncratic responses of different taxonomic groups. In addition, most of the European forests that are unmanaged today have undergone intensive management at some point in recent centuries. Nature conservationists and policy makers advocate the creation of new forest reserves which consist of setting aside parts of managed forests (Parviainen et al. 2000). This strategy relies on the assumption that the lack of forest management might benefit many forest-dwelling species. However, biodiversity recovery after stopping forest management may be slow, and the benefits of setting up new forest reserves may not be immediate. An estimate of the time needed for biodiversity recovery is thus crucial for conservation policy. In addition, forest management covers a large range of practices that likely have contrasting impacts on biodiversity: in coherence with our assumption on the negative impact of forest management *per se*, we can assume that the more intense the management, the higher the difference of biodiversity between unmanaged and managed forests (*e.g.* Stephens & Wagner 2007).

It is essential to review the scientific knowledge concerning the effect of absence or abandonment of management on forest ecosystems in order to highlight general ecological patterns. Although reviews have already been published, none have used a meta-analysis approach (*e.g.* Niemelä et al. 2007; Stephens & Wagner 2007). Here, we used meta-analysis to identify knowledge gaps on the biodiversity response to forest management in Europe. This review was drafted to support conservation policy and decision-making.

Meta-analysis is a method for analyzing and synthesizing the results of multiple independent studies that address the same question (Arnqvist & Wooster 1995; Gurevitch et al. 2001). Treatment effects can be quantitatively analyzed by this statistical procedure. The use of a common metric called "effect size" accounts for the fact that studies are not all equally reliable, *i.e.* studies with small sample sizes have lower statistical power than studies with large ones (Gurevitch et al. 2001). Since effect size is not sample size-dependent, it enables us to compare studies with different metrics or scales of measurement (Gurevitch et al. 2001). Meta-analysis is especially useful for examining general patterns of treatment effects in ecology (see *e.g.* Bengtsson et al. 2005; Jactel & Brockerhoff 2007; Zvereva et al. 2008).

We restricted our literature review to European forests in order to obtain a relatively homogeneous sample in terms of biogeography and phylogeography. We use species richness as a surrogate for biodiversity, as it is one of the simplest and widely-used ways to measure biological diversity (Noss 1990). However, this approach can sometimes be misleading as it does not fully describe biodiversity (Magura et al. 2001; Standovar et al. 2006).

This meta-analysis set out to answer the following questions:

(1) Is species richness systematically higher in unmanaged than in managed forests and/or does the effect of forest management vary widely with taxonomic/ecological group?

(2) For a given taxonomic/ecological group, does species richness change with time since abandonment, in line with a gradual recovery of the typical habitat conditions of unmanaged forests?

(3) For a given taxonomic/ecological group, does the difference in species richness between unmanaged and managed forests increase with management intensity?

Materials and methods

Data selection

We followed the guidelines for systematic literature reviews provided by Pullin & Stewart (2006) (see Supplementary Material). To be included in the analysis, a paper had to report summary data (*i.e.* mean, standard deviation and sample size) for species richness by comparing managed *vs.* unmanaged treatments. We selected 49 papers published between 1978 and 2007 (Table 1). These selected publications contained 120 comparisons (hereafter termed "individual studies"; see Supplementary Material). Unpublished material and grey literature were not included in the dataset.

In the selected papers, the term "forest management" encompassed any anthropogenic pressures related to direct forest resource use such as thinning, clearfelling, selective felling, any form of tree retention, grazing or planting (Table 1). Human impacts such as pollution, eutrophication, climate change or other indirect pressures were not considered. Most of the forests considered as unmanaged had not been influenced by direct human disturbance for at least 20 years. Studies with no detailed information on time since abandonment but that explicitly referred to an unmanaged old-growth stand (or a synonym such as "near-natural", "sub-natural" *sensu* Peterken, 1996) were also included.

The individual studies that compared mature forests and young regeneration phase or clearfellings were excluded, since these early short-term phases are known to be very different from older phases, regardless of whether or not they are managed. However, individual studies were included in the analysis when similar managed and unmanaged successional phases following natural disturbances were compared, *i.e.*: young managed *vs.* young unmanaged, old managed *vs.* old unmanaged.

We used species richness as a quantitative index in our analysis, although it represents only one aspect of biodiversity (Noss 1990).

Data treatments and calculations

For each comparison, mean species richness, standard deviation and sample size for each group were tabulated (see Supplementary Material). Data were extracted from the text, tables or graphs. The Hedges' *d* effect size (Equation 1) defines the standardized difference between mean species richness of managed forests (experimental group, $\overline{X}^E$) and unmanaged forests (control group, $\overline{X}^C$) divided by the pooled standard deviation (*S*, Equation 2) and multiplied by a correction factor (*J*, Equation 3):

$$d = J \frac{\overline{X}^E - \overline{X}^C}{S} \qquad \text{(Equation 1)}$$

$$S = \sqrt{\frac{(N^E - 1)(S^E)^2 + (N^C - 1)(S^C)^2}{N^E + N^C - 2}} \qquad \text{(Equation 2)}$$

$$J = 1 - \frac{3}{4(N^C + N^E - 2) - 1} \qquad \text{(Equation 3)}$$

where N^E and N^C are the sample sizes of the experimental and control groups and S^E and S^C are their standard deviations.

A negative *d* value means higher species richness in unmanaged than in managed forests. Effect sizes across all studies were combined to provide the grand mean effect size (d_{++}) (Gurevitch & Hedges 1999). We also calculated the log response ratio ($\ln R = \frac{\ln(\overline{S}^E)}{\ln(\overline{S}^C)}$) which gives an estimate of the percentage of variation in species richness between managed and unmanaged forests. Following Pullin & Stewart (2006), we opted for random-effects models rather than fixed-effects models, since ecological data are more subject to uncontrolled variations than data in other scientific fields such as medicine. The effect was considered statistically significant if the 95% bootstrap confidence interval, calculated with 999 iterations, did not bracket zero. We checked our dataset for the "file drawer problem" or publication bias using Spearman rank-order correlation (effect vs. variance). This test accounts for the fact that non-significant studies are less often published than those reporting significant results (Arnqvist & Wooster 1995).

We calculated a grand mean effect size (d_{++}) and a 95% bootstrap confidence interval for the 120 individual studies taken together. Each individual study was then assigned to a taxonomic or ecological group: the classification followed the classical Linnaean hierarchical taxonomy for most of the studies (Table 1). Beetles other than carabids were divided into two ecological groups: (1) saproxylic beetles, *i.e.* species that depend on deadwood during some part of their life-cycle (Speight 1989), and (2) non-saproxylic beetles. As we expected heterogeneous results for higher taxonomic levels (*e.g.* kingdom), we only analyzed elementary groups if they contained at least two individual studies (Table 1). An effect size (d_+) for each taxonomic group was calculated using random-effects model. The total heterogeneity Q_T of each group was tested against a chi-square distribution and the group was considered heterogeneous if $p(Q_T) < 0.05$.

We analyzed the effect of census plot area on the variability of the response of vascular plants to forest management using a continuous random-effects model and a log-transformation for plot area.

We then examined two factors: (1) for each study, time since abandonment (TSA) of management in the unmanaged forest was tabulated when available and we analyzed the global response as well as the response for each taxon using a continuous random-effects model; studies devoid of information on TSA were not included in this analysis; (2) we defined four classes of management types, ranked in the following decreasing gradient of management intensity:

- "clear-cut with species change": clear-cut forests with tree species composition change (native and non-native species);
- "clear-cut without species change": clear-cut forests without tree species change, including natural regeneration and plantations without species change;
- "selective felling": forests managed by selective felling (continuous cover), without reference to "close-to-nature" management;
- "selective felling close-to-nature": forest managed by selective felling with reference to "close-to-nature" management.

When possible, each study was assigned to one type of forest management (20 studies were not classified in any management type due to overly vague data). Grazing concerned only one article (Hansson 2001) and was not included in the analysis. We analyzed the global response and the response of each taxonomic group using mixed-effects models. The significance of the mean effect size for a taxonomic group (d_+) was tested by calculating a 95% bootstrap confidence interval (999 iterations). The effect was considered significant if the 95% bootstrap CI did not bracket 0. Variation in effect sizes across management types was explored by calculating between-class heterogeneity (Q_B) and tested against a chi-square distribution. If the result was significant ($p(Q_B) < 0.05$), the effect sizes of the different classes were significantly different.

MetaWin 2.1 software (Rosenberg et al. 2000) was used for the meta-analysis.

Results

General data structure and publication bias

Our dataset comprised 120 comparisons (individual studies) between managed and unmanaged forests (Table 1). The number of comparisons for each paper averaged 2.5 (±SD=2.1) and ranged from one to nine. The studies were equally distributed between plants and animals, but only twelve studies concerned fungi. Of the studies on animals, 86% dealt with arthropods, mainly *Coleoptera*.

There were twice as many studies in boreal than in temperate forests, but the taxonomic groups studied differed widely between biomes: 60% of the studies on vascular plants were conducted in temperate forests, whereas bryophytes and lichens were almost exclusively studied in boreal forests. Similarly, 74% of the studies on *Coleoptera* were conducted in boreal forests.

TSA varied from 10 to 160 years for 89 studies. Twenty-three studies, mainly located in the boreal zone, referred to old-growth stands without precision on TSA.

In terms of management type, a majority of studies fell into the "clear-cut without species change" and "selective felling" classes (33 and 38 respectively), whereas 12 comparisons concerned the "clear-cut with species change" class and 17 the "selective felling close-to-nature" class.

The Spearman rank correlation test performed on the whole dataset gave non-significant results ($Rs = -0.006$, $p = 0.945$) indicating no publication bias. As we expected contrasting responses for the different taxonomic groups, publication bias was also checked for the three kingdoms (plants, animals and fungi). Non-significant results were obtained for all three kingdoms: plants: *Rs* = 0.121 (*p* = 0.376); animals *Rs* = -0.036 (*p* = 0.802) and fungi: *Rs* = -0.168 (*p* = 0.602).

Meta-analysis

Overall effect size and effect size for the different taxonomic groups (Table 2)

Species richness was higher in unmanaged than in managed forests, as indicated by the negative grand mean calculated for the whole dataset (Table 2, Figure 1). However, the effect was only marginally significant (the upper boundary of bootstrap confidence interval was close to zero) and the response was strongly heterogeneous ($p(Q_T) < 0.001$). The mean effect size measured with the log ratio was -0.070, indicating that forest management globally decreased species richness by 6.8% (Table 2).

Taxonomic and ecological groups displayed contrasting responses to forest management (Table 2). Globally, the absolute values of effect size fell between 0.4 and 0.7 (except for carabids), which corresponds to a medium intensity effect (*sensu* Cohen 1969). The calculation of the log response ratio showed variation percentages from -30% to +13% (Table 2). Vascular plants and non-saproxylic beetles showed indications of higher species richness in managed forests, but the result was only marginally significant for vascular plants and was non-significant for non-saproxylic beetles. All the other groups exhibited higher species richness in the unmanaged forests but the results were only significant for fungi, lichens, carabids and saproxylic beetles. Bryophytes showed marginally significant differences while the other groups (birds, all arthropods, acari oribatids) yielded non-significant results. Total heterogeneity (Q_T) was never significant.

Plot area effect on vascular plant response

We analyzed 21 individual studies (out of the 28 available). Census plot area for vascular plants ranged from 4 m² to 400 m². There was no significant effect of plot area on effect size (*p* = 0.11).

Effect of time since abandonment (Table 3, figure 2)

We analyzed 89 individual studies (out of the 120 available). The global effect of TSA was significant and the slope of the regression was negative (Figure 2). The regression showed that the difference in species richness between managed and unmanaged forests was positive before 20 years and negative thereafter. This means that the older the management abandonment, the higher the species richness in unmanaged than in managed forests. For taxonomic groups, only carabids, saproxylic beetles and fungi showed significant results (Table 3). According to the regression equations, species richness became higher in unmanaged forests around 18 and 43 years after management abandonment for carabids and fungi respectively. For saproxylic beetles, species richness was higher in unmanaged forests whatever the TSA since the intercept was negative.

Effect of management type (Table 4)

We analyzed the effect of management type from 100 individual studies. When all taxa were included, mean effect sizes differed marginally among the management types. "Clear-cut with tree species change" showed the strongest negative impact. Along the rest of the management gradient, there was no clear trend: species richness was not affected by management in the "clear-cut without species change" type, but was slightly negatively affected in the "selective felling” and "selective felling close-to-nature" types.

When the dataset was divided into taxonomic groups, only bryophytes and lichens showed significant differences between management types: "selective felling" and "selective felling close-to-nature" significantly decrease the species richness of bryophytes and "selective felling" significantly decreases the species richness of lichens. For all the other groups, there were no significant differences between management types. However, these results have a low statistical power because of the limited number of individual studies in each type.

Discussion

Taxonomic groups showed contrasting responses to forest management

This quantitative review highlights a small, marginally significant effect of forest management on total species richness. Species richness tended to be higher in unmanaged than in managed forests, but the response varied widely among taxonomic groups.

Several mechanisms have been suggested to explain the effect of management on forest biodiversity: (1) changes in tree age structure, vertical stratification and tree species composition, which affect light, temperature, moisture, litter and topsoil conditions (Sebastia et al. 2005; Standovar et al. 2006); (2) presence of micro-habitats (*e.g.* deadwood, veteran trees, cavities, root plates) specific to unmanaged (Berg et al. 1994; Bouget 2005a; Christensen et al. 2005; Gibb et al. 2005) or managed forests (*e.g.* skid trails and haul roads) (Gosselin 2004; Hansen et al. 1991); (3) forest cover continuity and features resulting from extensive management in the past (Hjalten et al. 2007). The pattern of response may therefore depend on which of the above mechanisms, or which combinations of them, have the strongest effects on different taxonomic or functional groups.

Saproxylic beetles, bryophytes, lichens and fungi showed significantly or marginally significantly higher species richness in unmanaged forests in our meta-analysis. These substrate-dependent taxa suffer from the reduction of micro-habitat availability and diversity in managed forests. First, the quantitative and qualitative features of deadwood, the presence of large logs and snags, and the presence of different decay stages are key elements for these taxa (Bouget 2005b; Hjalten et al. 2007; Johansson et al. 2007; Odor et al. 2006). Second, fine-scaled soil disturbances following natural forest stand dynamics (*e.g.* establishment of pits, mounds and root plates) considerably increase the diversity of several taxa such as bryophytes and lichens (Jonsson & Esseen 1990; Kimmerer 2005). Lastly, micro-habitat continuity is especially important for dispersal-limited groups that are favored by stable conditions, *e.g.* for some red-listed bryophytes, lichens and fungi (Berg et al. 1994; Gustafsson et al. 2005). Carabid beetles showed the same response pattern but are probably less substrate-dependent and more influenced by landscape features (Niemelä et al. 2007). Indeed, studies dealing with carabids focused on comparisons of unmanaged forest remnants in a cultural landscape, which implied a strong confounding edge effect for this group.

Conversely, the species richness of vascular plants tended to be higher in managed forests although the response was heterogeneous. Frequent disturbances in managed forests such as canopy openings, litter removal and soil disturbance, all strongly favor many understory vascular plants, especially shade-intolerant, ruderal and/or competitive species but they can also favor shade-tolerant and/or stress-tolerant species (Brunet et al. 1996; Schmidt 2005). This generally results in an increase in total species richness. However, stand age, in relation to natural forest dynamics, may also influence the species richness of vascular plants (see below).

Forest management effect changes with time since abandonment

The TSA in unmanaged forests significantly influenced effect size: in the first twenty years, species richness was higher in managed than unmanaged forests, then after the 20-year cutoff, older management abandonment led to higher species richness in unmanaged forests. These variations could be linked to changes in forest conditions and structures (Fenton & Bergeron 2008). Almost all forests in Europe, except north Fennoscandia, have been intensively managed for centuries. Many forests currently considered as unmanaged have often been managed in the past (Bengtsson et al. 2000). For saproxylic beetles and fungi (the two groups for which TSA had a significant effect), the increasing abundance of micro-habitats in unmanaged forests can increase species richness. However, other substrate-dependent groups such as lichens and bryophytes were not significantly influenced by TSA. Consequently, our results partly support the idea that, after management stops, the dynamics of the ecosystem gradually restore appropriate conditions for the recolonisation of species that are dependent on typical unmanaged forest substrates.

However, the gradual recovery of biodiversity also depends on the regional species pool and the dispersal ability of species, which requires spatial and temporal continuity of forest features. Recolonisation by forest specialists can be very difficult even if the stand is left unmanaged for a long time. For example, dispersal limitation has been shown to be a key factor in the lichen dependence on old-growth forests in the United States (Sillett et al. 2000). The same pattern has been observed in the Atlantic forest reserves of Europe, where deadwood discontinuity may explain the absence of dispersal-limited epixylic bryophytes, which need relatively long intervals to recolonize the younger reserves (Odor et al. 2006).

Unclear effect of management intensity

According to our main hypothesis, we expected that the more intense the forest management, the higher the species richness difference between unmanaged and managed forests. Indeed, our results showed that the effect of forest management varied with the type of management. In comparison with the unmanaged reference, the strongest difference in species richness was observed for forests that have undergone clear-cut and tree species change in the past (Stephens & Wagner 2007). Conversely, species richness of forests clear-cut in the past but without species change (natural and/or artificial regeneration) did not differ from unmanaged references. Clear-cutting is typical of boreal forests, as it mimics the natural fire-disturbance regime. However, clear-cutting may diverge strongly from natural fire regime with respect to disturbance intensity and frequency and influence on habitat characteristics; the effects of management on biodiversity may thus be higher than those shown by our results (*e.g.* Niemelä et al. 2007). The effect of selective cuttings, whether close-to-nature or not, was not significant. Our analysis of the effect of management types for each taxonomic group could not highlight clear and statistically powerful trends due to the low number of replications in each class. It was also impossible to test the interaction between management type and TSA, but this would still have raised the problem of low replication number.

Our results suggest that large and intense disturbances followed by tree species composition change have the strongest detrimental effect on species richness. The rest of the management intensity gradient showed no clear trend.

Possible confounding effects and limitations in the meta-analysis approach

The low significance level of our results could have several explanations, including a lack of control of confounding factors in the sampling design and our approach, which was based on total species richness.

The lack of reported information on possible confounding factors and the difficulty of controlling some of them in the field did not allow us to test their effects. Forest site (topography and soil types) was generally controlled whereas the control of tree species composition and stand age or successional phases was less rigorous. Moreover, since forest management *per se* influences tree composition and stand age or succession, we considered that these factors did not have to be systematically controlled.

Differences in patch size and landscape patterns, past land use and management history between unmanaged and managed forests may have an effect on species richness. The studies analyzed here rarely adopted a sampling design based on matched landscapes (*e.g.* paired plots) and information on the spatial structure of the design and the surface area of the sampled forest units was often lacking (only 4 individual studies controlled landscape). Indeed, the effect of adjacent landscape structure could override the forest management effect, especially for mobile groups such as birds and carabids, since the population dynamics of many organisms operate at a larger scales than the forest stand (Brotons et al. 2003; Helle 1986; Lohmus 2004; Magura et al. 2000). Compared with managed forests, most of the unmanaged patches are probably too small to be considered as fully independent forest ecosystems (Graae & Heskjaer 1997). Such small areas are not suitable for maintaining populations of species that depend on unmanaged forest features and do not contain all the stages that compose a natural forest succession (*e.g.* Koop & Hilgen 1987; Szwagrzyk & Czerwczak 1993). Also, unmanaged stands are often surrounded by a matrix of managed forest; community species richness and composition in the unmanaged patches may thus be strongly influenced by the neighboring managed forest matrix. Too little edge distance between felled stands and unmanaged areas could prevent forest-interior specialists from surviving (Niemelä et al. 2007; Spence et al. 1996). For birds in particular, generalist species can be favored by increased competition rates and/or decreased availability of nesting and feeding habitats (Lohmus 2004). In addition, recent research has underlined the visible effect of past land use on forest plant diversity and chemical soil properties (Verheyen et al. 2003), even several centuries after human occupation (*e.g.* Dambrine et al. 2007).

Another limitation in our meta-analysis is its reliance on the use of plot-level species richness as a surrogate for biodiversity.

Firstly, analyzing overall species richness may be misleading and may disguise basic ecological processes (Magura et al. 2001). It would therefore be more meaningful to focus on species traits and analyze the species richness of each ecological group (Bernhardt-Romermann et al. 2008; Johansson et al. 2007; Kolb & Diekmann 2005), *i.e.* herbivorous *vs.* predators or saproxylic *vs.* non-saproxylic beetles (Martikainen et al. 2006), neotropical *vs.* paleotropical migrant birds (Hansson 2001) or forest *vs.* open habitat species (Magura et al. 2001; Niemelä et al. 2007). However, this kind of approach can be difficult to apply in a meta-analysis because functional-trait based species classifications often vary between authors and countries. Similarly, it would be interesting to focus on species composition and determine which species are more frequent or abundant in unmanaged forests than in managed forests. In particular, intensive forest management may affect more forest specialists than other groups. This approach would require the original dataset of each study, *i.e.* the plot-species matrix.

Second, census plot area can vary widely between studies but we did not detect an effect of plot area on the response of vascular plants to forest management. The calculation of effect size already standardizes differences in plot area species richness (Gurevitch et al. 2001), so the detection of an effect of plot area would imply that species richness differences were scale-dependent. Since forest is a mosaic of dynamic ecosystems (Spies & Turner 1999), the alpha-diversity index considered here is an incomplete descriptor of the management effect; it would certainly be more appropriate to compare alpha-, beta- and gamma-diversity between managed and unmanaged forest landscapes. For example, plant communities studies have found that unmanaged forests displayed a higher beta-diversity of plant communities due to higher within-stand habitat heterogeneity (Bobiec 1998) and that the observed difference between unmanaged and managed sites is strongly dependent on spatial scale (Standovar et al. 2006). It would also be interesting to analyze the scale dependence of the species richness response for other taxonomic groups, although it may be difficult to define plot area for species like arthropods.

Implications for research, forest management and conservation policy

Research gap

Although the first step in the literature search was fruitful, the number of studies suitable for meta-analysis proved much smaller than expected. Many studies were purely descriptive, rather than comparative, and/or did not report species richness summary data. In addition, many studies dealt with other descriptors of biodiversity than species richness, such as biomass for ungulates (Jedrzejewska et al. 1994), number of pairs per area unit for birds (Kouki & Vaananen 2000; Virkkala & Rajasarkka 2006) or abundance or species composition for insects (Simila et al. 2003; Vaisanen et al. 1993). Another critical problem in the literature selection was the relatively scant reporting of summary statistics (standard deviation and sample size) in the published papers not only in old, but also in recent publications. This problem has already arisen in other meta-analyses on biodiversity (*e.g.* Bengtsson et al. 2005; Zvereva et al. 2008). Our results suggest that scientific journals should edit their instructions to authors to ask for mean values to be presented along with their corresponding variance, which would facilitate future bibliographic reviews and meta-analysis. We also agree with the arguments of Pärtel (2006) and recommend that a complete list of species for each sample site be systematically included in either the publication or in the electronic archives.

Although the structure of our sample was closely dependent on the selection criteria (in our case species richness), we highlight a critical knowledge gap concerning several important taxa in Europe. There were few reports on arachnids, mollusks and soil and none at all on bats or small mammals. Also, the Mediterranean zone, France and Poland were underrepresented. Studies on taxa that provided significant results in our meta-analysis, such as bryophytes, lichens or saproxylic beetles were restricted to Fennoscandia. These taxa should also be studied in the temperate biome to test the effect of forest management. It would also be useful to rigorously test the effect of a TSA gradient on the same study area in future research projects, in order to more accurately evaluate the time needed for biodiversity to recover after management stops. We also suggest that authors systematically provide detailed information on forest site, stand characteristics, plot area, landscape structure, past land use and management history as it is important to control the influence of these possible confounding factors in sampling strategies. Finally, as stated above, we emphasize the need to analyze the species composition response to forest management and to use functional classifications to determine which species traits can be favored or disfavored by management.

Implications for forest management and conservation policy

Our meta-analysis is the first to deal with the effects of forest management on species richness. Our results provide arguments for the conservation of unmanaged forests and the creation of forest reserves on a broad scale. We also showed that the time of abandonment needed for the biodiversity to recover varies from 18 to more than 40 years, depending on the taxa. Although our results have to be confirmed by complementary studies, we hence emphasize that the time required for recovery of the biodiversity in unmanaged forests may prove particularly long for several groups, which means that the efficiency of conservation policy needs to be assessed within a long-term perspective.

The conservation priority needs to focus on saproxylic beetles, bryophytes, lichens, carabids and fungi, as these taxa proved to be the most sensitive to forest management. However, other taxonomic groups also need to be monitored, since there were few studies available on these groups for our meta-analysis. More generally, as different taxa may respond differently to forest management, the conservation priority has to focus on taxa for which habitats are the more threatened by forest management (*e.g.* dead wood).

We finally strongly support the creation of a coordinated monitoring network to compare biodiversity between unmanaged and managed forests (Larsson 2001; Meyer 2005; Parviainen et al. 2000). This kind of network would provide not only basic information such as species richness for several taxonomic groups, but also more fundamental knowledge on the patterns and processes involved in forest biodiversity.

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Supplementary Material

Bibliographic review method and English keywords used for database interrogations (Appendix S1), Summary of the data included in the meta-analyses (Appendix S2) and References used for the meta-analysis (Appendix S3) are available as part of the on-line article from http://www.blackwell-synergy.com/. The authors are responsible for the content and functionality of these materials. Queries (other than absence of the material) should be directed to the corresponding author.

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Table 1. Data structure (individual studies). The table includes all the studies referenced in the bibliographic review. Some groups were not analyzed because they included only one comparison and/or were from only one study, *i.e.*: vascular plants and bryophytes, all arthropods together, *Acari oribatids, Araneae, Curculionidea*.

	Management type					**Biome**		**Total**
	Clear-cut with sp. change[d]	**Clear-cut without sp. change**[e]	**Selective felling**[f]	**Selective felling close-to-nature**[g]	**UD**[h]	**Boreal**	**Temperate**	
All	**12**	**33**	**38**	**17**	**20**	**84**	**36**	**120**
Plants	**4**	**21**	**17**	**6**	**8**	**37**	**19**	**56**
Bryophytes		6	2	2	4	12	2	14
Lichens		8	4	1		13		13
Vascular[a]	4	7	10	3	4	12	16	28
Vascular[a] & bryophytes			1				1	1
Animals	**8**	**12**	**15**	**6**	**11**	**36**	**16**	**52**
Acari Oribatids					3		3	3
All arthropods[b]		1	3	1		4	1	5
Araneae spiders			1			1		1
Birds	1		3	2	2	5	3	8
Carabids	5	1			2		8	8
Coleoptera, Curculionidea			1				1	1
Diptera, mycetophilidae					1	1		1
Non-saproxylic beetles	1	5	1	1		8		8
Saproxylic beetles[c]	1	5	6	2	3	17		17
Fungi			**6**	**5**	**1**	**11**	**1**	**12**

[a] including ferns
[b] this group derives from studies without taxonomic distinction within the group
[c] including bark beetles
[d] clear-cut forests with tree species change
[e] clear-cut forests without tree species change, including natural regeneration and plantations without species change
[f] forests managed by selective felling (continuous cover), without reference to "close-to-nature" management
[g] forest managed by selective felling with reference to "close-to-nature" management
[h] undetermined type

Table 2. Analysis of the effect of forest management on total species richness and species richness of different taxonomic groups[a].. Average *d*: Hedges' *d* effect size. d_{++} is the grand mean and d_{+} is the mean of a taxonomic group. Bootstrap CI: 95% bootstrap confidence interval calculated with 999 iterations. *n*: number of individual comparisons. Q_T: total heterogeneity. $p(Q_T)$: heterogeneity is tested against a chi-square distribution. %variation: difference of species number between managed and unmanaged forests expressed as a percentage calculated with the log response ratio.

	Average d	**Bootstrap CI**					**%variation**
	d_{+} *or* d_{++}	**-**	**+**	**n**	Q_T	$p(Q_T)$	
All	**-0.24(*)**	**-0.48**	**-0.03**	**120**	**183.41**	**<0.0001**	**-6.8%**
Vascular plants[b]	0.47(*)	-0.01	0.91	28	39.64	0.06	12.7%
Bryophytes	-0.46(*)	-0.97	-0.04	14	18.51	0.14	-21.0%
Lichens	-0.40*	-0.79	-0.10	13	12.35	0.42	-8.6%
Birds	-0.21	-0.52	0.36	8	10.48	0.16	-7.7%
All Arthropods	0.12	-0.63	1.10	5	4.44	0.35	1.6%
Acari oribatids	-0.25	-1.08	0.51	3	2.03	0.36	-8.3%
Carabids	-1.98*	-3.34	-0.56	8	7.45	0.38	-29.8%
Saproxylic beetles[c]	-0.67*	-1.19	-0.25	17	17.43	0.36	-17.5%
Non-saproxylic beetles	0.37	-0.29	0.97	8	5.91	0.55	8.4%
Fungi	-0.65*	-1.25	-0.13	12	14.77	0.19	-17.5%

* significant effect; (*) marginally significant effect

[a] one study gave the Shannon index in place of species richness but was included anyway (Vellak & Paal 1999, see Supplementary Material)

[b] including ferns

[c] including bark beetles

Table 3. Meta-analysis of the response to forest management of each taxonomic group with respect to time since abandonment (TSA)[a]. SE: Standard Error; p: probability was tested against a normal distribution; n: number of individual studies.

	Intercept (±SE)	**Slope (±SE)**	***p***	**n**	**TSA range (min – max)**
All	**0.1222 (±0.2152)**	**-0.0059 (±0.0025)**	**0.0018**	**89**	**10 – 160**
Vascular plants[b]	0.7618 (±0.3191)	-0.0037 (±0.0046)	0.43	23	10 – 140
Bryophytes	-0.5462 (±0.5274)	0.0057 (±0.0084)	0.50	8	14 – 100
Lichens	0.4358 (±0.9169)	-0.0083 (±0.0086)	0.39	10	50 – 120
Birds	-0.7277 (±0.4675)	0.0063 (±0.0070)	0.37	7	30 – 100
Carabids	1.3931 (±0.4785)	-0.0782 (±0.0027)	0.004	6	42 – 70
Saproxylic beetles[c]	-0.1997 (±0.4479)	-0.0094 (0.0041)	0.02	12	40 – 160
Non-saproxylic beetles	1.1565 (±0.7382)	-0.0098 (±0.0061)	0.11	6	50 – 160
Fungi	0.8720 (±0.5972)	-0.0202 (±0.0071)	0.005	11	50 – 160

[a] The TSA effect was analyzed via a continuous random-effects model
[b] including ferns
[c] including bark beetles

Table 4. Analysis of the response to forest management of each taxonomic group with respect to type of management. The groups included in these analyses contained at least two individual studies in each management class. d_+: Hedges' d effect size for each management type; n: number of individual comparisons; Q_B: between group heterogeneity; $p(Q_B)$: heterogeneity was tested against a chi-square distribution.

	Clear-cut with sp. change		**Clear-cut without sp. change**		**Selective felling**		**Selective felling close-to-nature**			
	d_+	n	d_+	n	d_+	n	d_+	n	Q_B	$p(Q_B)$
All	**-1.08***	**12**	**0.02**	**33**	**-0.38(*)**	**38**	**-0.29**	**17**	**7.67**	**0.053**
Vascular plants[1]	0.84*	4	0.21	7	0.21	10	1.25*	3	4.03	0.259
Bryophytes			0.09	6	-1.95*	2	-0.62*	2	11.26	0.004
Lichens			-0.14	8	-0.83*	4			3.05	0.081
Birds					-0.03	3	-0.67*	2	2.66	0.103
Saproxylic beetles[2]			-0.36	5	-1.14*	6	-1.27*	2	1.53	0.465
Fungi					-0.44	6	-0.97*	5	0.67	0.412

* significant effect, (*) marginally significant effect

[1] including ferns

[2] including bark beetles

Figure 1. Hedges' *d* effect size and variance (error bars) of individual studies comparing species richness between unmanaged and managed forests. A negative effect size means that species richness was higher in unmanaged forests than in managed forests. More information on each study is given in Supplementary Material.

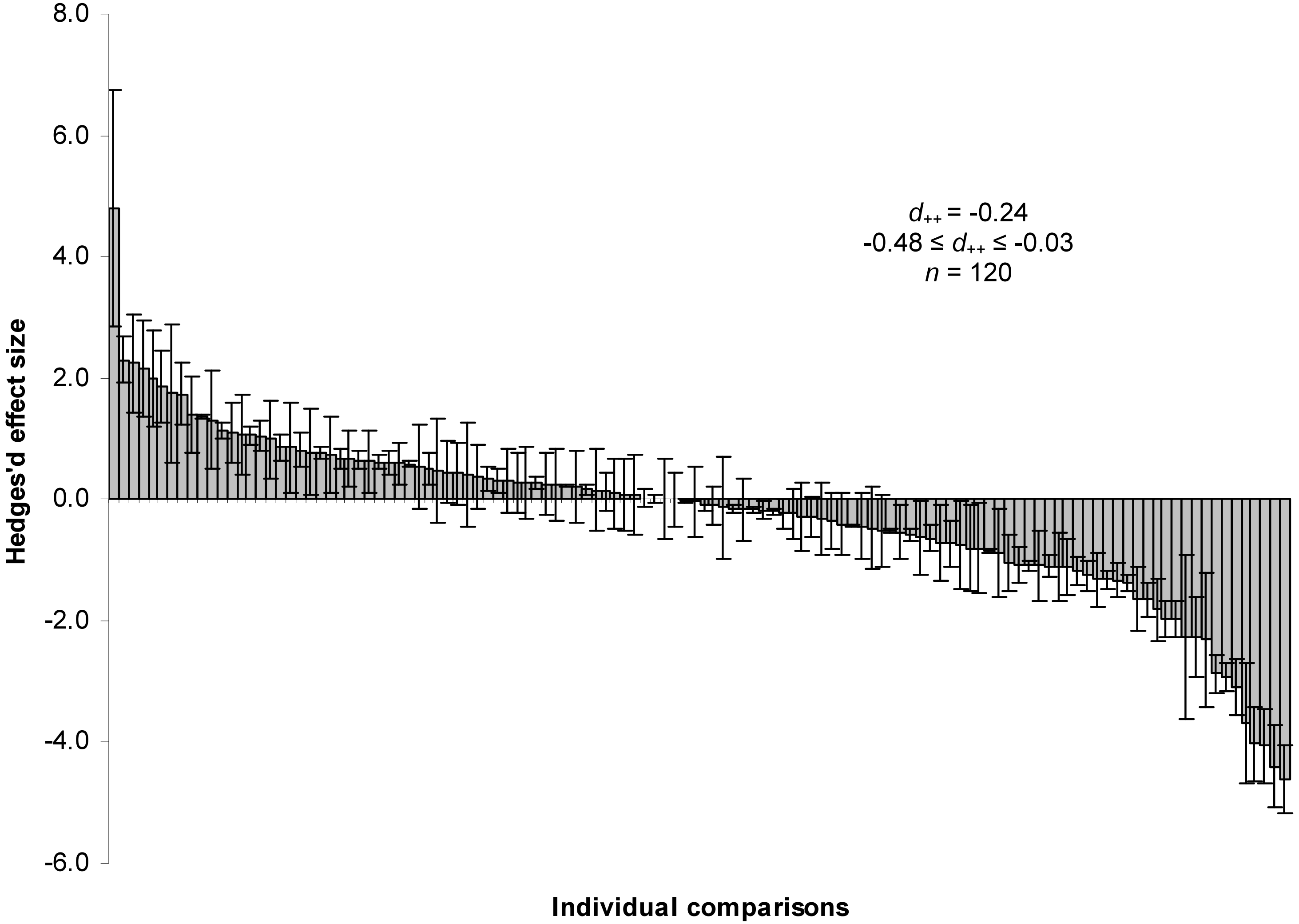
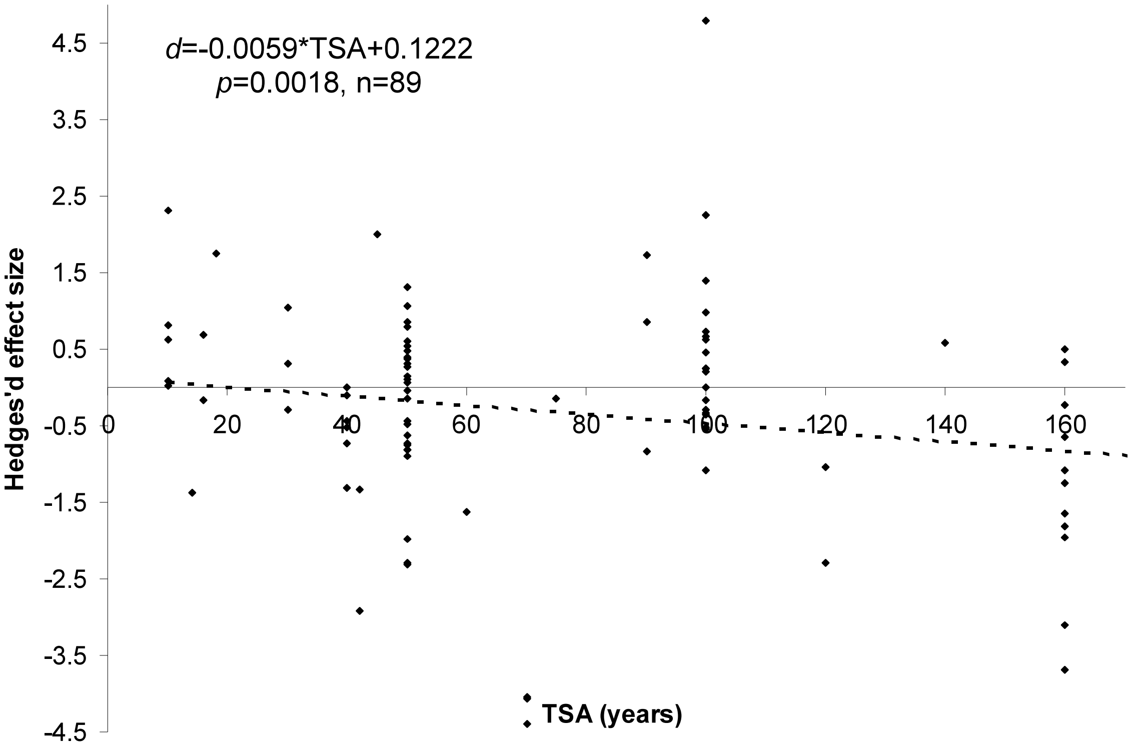


Figure 2. Regression plot of the effect of Time Since Abandonment (TSA) of management in the unmanaged forests on Hedges' *d* effect size. The TSA effect was analyzed via a continuous random-effects model; *p*: probability was tested against a normal distribution; n: number of individual studies. See table 3 for details.



Supplementary Material

Appendix S1. Bibliographic review method and English keywords used for database interrogations

Method:

We used the same English keywords to investigate different databases. We considered all the literature referenced on the Web of Science database (date queried: June 2007; only papers published since 1991), Zoological records database (date queried: March 2007; published between 1980 and 2006). The keywords used were broad enough to make sure they included all relevant papers (see below). A second step refined the selected list: based on title and abstract, we selected papers that explicitly mentioned a species richness-related comparison between managed and unmanaged forests in Europe. We also checked the references cited in the selected articles and, based on main author names of these selected articles, we also searched for publications on the Web of Science database. To be included in the analysis, the paper had to give summary data (*i.e.* mean, standard deviation and sample size) for species richness by comparing managed *vs.* unmanaged treatments. The authors were contacted by e-mail if any of these data were missing. Out of more than 500 checked papers published between 1978 and 2007, 49 matched our search criteria.

Database restrictions:

Publication year: no restriction: *Timespan=1991-2006*

Papers in English only: *DocType=Article; Language=English;*

Keywords used:

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Appendix S2. Summary of the data included in the meta-analysis.

	Article	Kingdom	Branch	Taxonomic / ecological group	Plot size (m^2)	TSA (years)	Management type	Hedges'*d*	$\overline{X}^C$	S^C	N^C	$\overline{X}^E$	S^E	N^E
1	Barkham (1992)	Plants	Vascular		4	18	Clear-cut with sp. change	1.76	7.8	2.2	3	13.9	3.0	2
2	Boncina (2000)	Plants	Vascular		16		Selective cutting close-to-nature	1.37	39.0	9.0	70	55.4	14.2	70
3	Chumak *et al.* (2005)	Animals	Arthropods	All arthropods			Selective cutting close-to-nature	2.15	181.5	9.7	4	229.3	25.5	4
4	Dettki & Esseen (1998)	Plants	Lichens		314	100	Clear-cut without sp. change	-0.28	13.5	0.7	2	12.6	3.1	20
5	Dettki & Esseen (1998)	Plants	Lichens		314	100	Clear-cut without sp. change	-0.17	16.4	1.7	71	16.1	1.8	38
6	Ebrecht & Schmidt (2001)	Plants	Vascular			16	Selective cutting close-to-nature	0.68	13.7	4.7	9	17.0	4.6	22
7	Ebrecht & Schmidt (2001)	Plants	Bryophytes			16	Selective cutting close-to-nature	-0.18	3.4	2.0	9	3.1	1.9	22
8	Erdmann *et al.* (2006)	Animals	Arthropods	Acari Oribatids		160		-0.23	9.0	2.8	8	8.4	2.1	8
9	Erdmann *et al.* (2006)	Animals	Arthropods	Acari Oribatids		160		-1.08	9.0	2.8	8	6.4	1.6	8
10	Erdmann *et al.* (2006)	Animals	Arthropods	Acari Oribatids		160		0.51	9.0	2.8	8	10.5	2.8	8
11	Esseen *et al.* (1996)	Plants	Lichens				Selective cutting	0.00	15.0	1.0	3	15.0	2.1	3
12	Gotmark *et al.* (2005)	Plants	Vascular			140	Selective cutting	0.59	20.0	4.6	6	23.4	5.9	6
13	Graae & Heskjaer (1997)	Plants	Vascular		5		Selective cutting	0.13	52.3	10.4	6	54.7	21.0	7
14	Hansson (2001)	Plants	Vascular		25	100		2.24	59.0	3.0	4	79.8	11.0	4
15	Hansson (2001)	Plants	Vascular		25	100		4.80	59.0	3.0	4	74.5	2.6	4
16	Hansson (2001)	Plants	Vascular		25	100	Selective cutting	0.45	59.0	3.0	4	62.5	9.0	4
17	Hansson (2001)	Animals	Birds			100		1.40	17.0	7.0	4	27.5	6.0	4
18	Hansson (2001)	Animals	Birds			100		0.62	17.0	7.0	4	22.3	7.8	4
19	Hansson (2001)	Animals	Birds			100	Selective cutting	0.26	17.0	7.0	4	19.0	6.6	4
20	Heino *et al.* (2005)	Plants	Bryophytes			14		-1.37	6.5	2.5	15	3.2	2.3	25
21	Helle (1986)	Animals	Birds			30	Clear-cut with sp. change	-0.28	27.3	4.2	6	25.7	6.4	6
22	Helliwell (1978)	Plants	Vascular				Selective cutting	0.58	27.0	11.0	21	35.0	14.1	102
23	Helliwell (1978)	Plants	Vascular				Clear-cut with sp. change	0.76	27.0	11.0	21	38.0	17.0	19
24	Hjalten *et al.* (2007)	Animals	Arthropods	Saproxylic beetles				0.27	6.9	7.4	20	9.1	8.7	20
25	Hjalten *et al.* (2007)	Animals	Arthropods	Saproxylic beetles				-0.10	6.9	7.4	20	6.2	7.4	20
26	Johansson *et al.* (2007)	Animals	Arthropods	Saproxylic beetles				0.16	12.6	4.4	27	13.3	4.6	27
27	Junninen *et al.* (2006)	Fungi				50	Selective cutting	1.31	20.0	2.2	3	25.6	4.3	3
28	Junninen *et al.* (2006)	Fungi				50	Selective cutting	0.40	22.5	3.5	2	29.4	15.2	3
29	Junninen *et al.* (2006)	Fungi				50	Selective cutting	-0.47	25.6	3.3	3	21.3	9.7	3
30	Junninen *et al.* (2006)	Fungi				50	Selective cutting close-to-nature	-0.14	20.0	2.2	2	19.5	3.2	3
31	Junninen *et al.* (2006)	Fungi				50	Selective cutting close-to-nature	-2.31	22.5	3.5	3	9.4	5.4	3

	Article	Kingdom	Branch	Taxonomic / ecological group	Plot size (m²)	TSA (years)	Management type	Hedges'*d*	$\overline{X}^C$	S^C	N^C	$\overline{X}^E$	S^E	N^E
32	Junninen *et al.* (2006)	Fungi				50	Selective cutting close-to-nature	-0.89	25.6	3.3	3	20.2	6.0	3
33	Junninen *et al.* (2006)	Fungi				50	Selective cutting close-to-nature	0.15	20.9	3.8	3	22.2	8.6	3
34	Junninen & Kouki (2006)	Fungi					Selective cutting	-0.60	4.2	2.4	72	2.8	1.8	12
35	Kuusinen & Siitonen (1998)	Plants	Lichens			120	Selective cutting	-1.05	88.0	7.0	5	78.0	10.0	5
36	Kuusinen & Siitonen (1998)	Plants	Lichens			120	Selective cutting	-2.28	88.0	7.0	5	69.0	8.0	5
37	Kuusinen (1994)	Plants	Lichens				Selective cutting	-0.24	32.5	3.8	13	31.3	8.7	3
38	Kuusinen (1994)	Plants	Lichens				Selective cutting close-to-nature	-1.33	32.5	3.8	13	26.1	6.2	6
39	Laiolo *et al.* (2003)	Animals	Birds			90	Selective cutting close-to-nature	-0.84	11.0	3.2	63	8.7	2.2	66
40	Laiolo *et al.* (2004)	Animals	Birds			40	Selective cutting	-0.43	3.5	1.4	166	2.9	1.4	89
41	Laiolo *et al.* (2004)	Animals	Birds			40	Selective cutting close-to-nature	-0.52	3.5	1.4	166	2.8	1.2	59
42	Lindblad (1998)	Fungi				75	Selective cutting	-0.15	8.4	31.6	36	4.7	12.0	36
43	Lohmus (2004)	Animals	Birds				Selective cutting	0.65	15.2	10.0	10	21.3	8.7	20
44	Magura *et al.* (2000)	Animals	Arthropods	Carabids		42	Clear-cut with sp. change	-2.92	9.7	2.2	18	3.4	2.0	18
45	Magura *et al.* (2000)	Animals	Arthropods	Carabids		42	Clear-cut with sp. change	-1.33	9.7	2.2	18	7.3	1.2	18
46	Magura *et al.* (2003)	Animals	Arthropods	Carabids		70	Clear-cut with sp. change	-4.03	14.3	1.6	10	8.1	1.3	10
47	Magura *et al.* (2003)	Animals	Arthropods	Carabids		70	Clear-cut with sp. change	-4.40	14.3	1.6	10	8.2	0.9	10
48	Magura *et al.* (2003)	Animals	Arthropods	Carabids		70	Clear-cut with sp. change	-4.06	14.3	1.6	10	8.6	1.0	10
49	Martikainen *et al.* (1996)	Animals	Arthropods	Bark beetles		40	Selective cutting	-1.32	8.8	3.0	5	5.5	1.5	6
50	Martikainen *et al.* (1996)	Animals	Arthropods	Bark beetles		40	Selective cutting	-0.73	10.5	2.5	6	8.5	2.5	5
51	Martikainen *et al.* (1996)	Animals	Arthropods	Bark beetles		40	Selective cutting	-0.10	5.7	2.0	7	5.5	1.5	6
52	Martikainen *et al.* (1996)	Animals	Arthropods	Bark beetles		40	Selective cutting	0.00	6.0	2.5	5	6.0	3.0	4
53	Martikainen *et al.* (1999)	Animals	Arthropods	Bark beetles		160	Selective cutting	-1.65	16.7	1.8	9	12.8	2.6	10
54	Martikainen *et al.* (1999)	Animals	Arthropods	Bark beetles		160	Selective cutting close-to-nature	-0.64	16.7	1.8	9	15.0	3.0	11
55	Martikainen *et al.* (2000)	Animals	Arthropods	Non-saproxylic		160	Selective cutting close-to-nature	0.34	83.9	7.8	9	87.8	12.9	11
56	Martikainen *et al.* (2000)	Animals	Arthropods	Non-saproxylic		160	Selective cutting	-1.25	83.9	7.8	9	74.0	7.3	10
57	Martikainen *et al.* (2000)	Animals	Arthropods	Saproxylic beetles		160	Selective cutting close-to-nature	-1.96	84.6	11.6	9	61.5	11.0	11
58	Martikainen *et al.* (2000)	Animals	Arthropods	Saproxylic beetles		160	Selective cutting	-3.10	84.6	11.6	9	50.8	9.2	10
59	Odor & Standovar (2001)	Plants	Bryophytes				Selective cutting	-2.88	15.9	6.4	8	3.8	2.7	20
60	Okland (1994)	Animals	Arthropods	Diptera, mycetophilidae		60		-1.63	28.0	9.3	5	15.6	2.9	5
61	Onaidia *et al.* (2004)	Plants	Vascular			100		0.00	9.2	2.5	32	9.2	3.1	32
62	Onaidia *et al.* (2004)	Plants	Vascular			100		-1.08	9.2	2.5	32	6.9	1.2	24
63	Onaidia & Amezaga (2000)	Plants	Vascular		4	30	Clear-cut with sp. change	0.32	8.2	3.5	9	9.5	4.2	12
64	Onaidia & Amezaga (2000)	Plants	Vascular		4	30	Clear-cut with sp. change	1.05	8.2	3.5	9	13.4	5.7	9
65	Penttila *et al.* (2004)	Fungi				160	Selective cutting	-3.69	45.7	5.6	6	25.4	4.2	5

	Article	Kingdom	Branch	Taxonomic / ecological group	Plot size (m²)	TSA (years)	Management type	Hedges'*d*	$\overline{X}^C$	S^C	N^C	$\overline{X}^E$	S^E	N^E
66	Penttila *et al.* (2004)	Fungi				160	Selective cutting close-to-nature	-1.81	45.7	5.6	6	33.0	7.3	5
67	Pettersson (1996)	Animals	Arthropods	Araneae spiders			Selective cutting	-1.12	6.8	3.1	5	3.4	2.3	5
68	Poole *et al.* (2003)	Animals	Arthropods	Carabids		50	Clear-cut without sp. change	-1.97	6.2	1.7	10	3.3	1.1	10
69	Poole *et al.* (2003)	Plants	Vascular			50	Clear-cut without sp. change	0.61	9.2	2.9	10	10.8	2.0	10
70	Schmidt (2005)	Plants	Vascular		100	10	Selective cutting	0.82	23.3	10.3	17	31.2	2.9	5
71	Schmidt (2005)	Plants	Vascular		100	10	Selective cutting	2.30	13.0	9.3	9	31.3	4.8	8
72	Schmidt (2005)	Plants	Vascular		100	10	Selective cutting	0.02	31.2	4.7	10	31.3	4.9	17
73	Schmidt (2005)	Plants	Vascular		100	10	Selective cutting	0.62	26.0	3.7	14	29.6	6.5	29
74	Schmidt (2005)	Plants	Vascular		100	10	Selective cutting	0.08	22.9	6.9	12	23.5	7.8	2
75	Sebastia *et al.* (2005)	Plants	Vascular		100	45	Selective cutting close-to-nature	1.99	26.6	6.8	5	40.0	3.3	3
76	Siira *et al.* (2003)	Animals	Arthropods	All arthropods			Selective cutting	0.43	15.0	4.0	4	17.0	4.0	4
77	Siira *et al.* (2003)	Animals	Arthropods	All arthropods			Selective cutting	-0.17	15.0	4.0	4	14.0	6.0	4
78	Siira *et al.* (2003)	Animals	Arthropods	All arthropods			Selective cutting	-0.41	15.0	4.0	4	12.0	8.0	4
79	Siira *et al.* (2003)	Animals	Arthropods	All arthropods			Clear-cut without sp. change	-1.09	15.0	4.0	4	10.0	4.0	4
80	Simila *et al.* (2002)	Animals	Arthropods	Saproxylic beetles		50	Clear-cut without sp. change	-0.75	56.3	11.7	3	40.0	21.7	3
81	Simila *et al.* (2002)	Animals	Arthropods	Non-saproxylic		50	Clear-cut without sp. change	0.78	33.7	3.5	3	41.3	10.4	3
82	Simila *et al.* (2002)	Animals	Arthropods	Saproxylic beetles		50	Clear-cut without sp. change	-2.28	45.0	5.7	2	24.3	7.0	3
83	Simila *et al.* (2002)	Animals	Arthropods	Non-saproxylic		50	Clear-cut without sp. change	0.48	36.5	2.1	2	39.3	5.0	3
84	Simila *et al.* (2002)	Animals	Arthropods	Saproxylic beetles		50	Clear-cut without sp. change	-0.80	39.3	12.9	3	28.3	8.6	3
85	Simila *et al.* (2002)	Animals	Arthropods	Non-saproxylic		50	Clear-cut without sp. change	0.53	32.3	2.1	3	37.3	10.4	3
86	Simila *et al.* (2002)	Animals	Arthropods	Saproxylic beetles		50	Clear-cut without sp. change	0.07	45.3	6.5	3	45.7	2.3	3
87	Simila *et al.* (2002)	Animals	Arthropods	Non-saproxylic		50	Clear-cut without sp. change	0.85	31.0	7.0	3	39.0	8.0	3
88	Sippola *et al.* (2002)	Animals	Arthropods	Saproxylic beetles			Clear-cut without sp. change	1.11	33.0	4.6	9	43.0	16.1	3
89	Sippola *et al.* (2002)	Animals	Arthropods	Saproxylic beetles			Clear-cut with sp. change	-1.11	40.0	6.1	6	33.0	4.0	3
90	Sippola *et al.* (2002)	Animals	Arthropods	Non-saproxylic			Clear-cut without sp. change	1.87	29.0	3.3	9	35.0	0.6	3
91	Sippola *et al.* (2002)	Animals	Arthropods	Non-saproxylic			Clear-cut with sp. change	0.28	30.0	7.0	6	32.0	4.6	3
92	Standovar *et al.* (2006)	Plants	Vascular		400		Selective cutting	-4.61	16.0	3.8	8	3.7	2.0	20
93	Strandberg *et al.* (2005)	Plants	Vascular and bryophytes		2.5	90	Selective cutting	1.74	3.0	2.0	3	10.1	4.1	13
94	Uotila *et al.* (2005)	Plants	Vascular		10	50	Clear-cut without sp. change	0.31	6.4	2.9	5	7.3	2.1	3
95	Uotila *et al.* (2005)	Plants	Vascular		10	50	Clear-cut without sp. change	-0.73	9.3	4.7	4	6.0	1.7	3
96	Uotila *et al.* (2005)	Plants	Vascular		10	50	Clear-cut without sp. change	-0.04	9.0	9.4	4	8.7	2.3	3
97	Uotila *et al.* (2005)	Plants	Bryophytes		10	50	Clear-cut without sp. change	0.37	7.0	0.7	5	7.7	2.5	3
98	Uotila *et al.* (2005)	Plants	Bryophytes		10	50	Clear-cut without sp. change	0.09	8.5	1.9	4	8.7	0.6	3
99	Uotila *et al.* (2005)	Plants	Bryophytes		10	50	Clear-cut without sp. change	1.07	7.0	1.2	4	8.7	1.5	3

	Article	Kingdom	Branch	Taxonomic / ecological group	Plot size (m²)	TSA (years)	Management type	Hedges'*d*	$\overline{X}^C$	S^C	N^C	$\overline{X}^E$	S^E	N^E
100	Uotila *et al.* (2005)	Plants	Lichens		10	50	Clear-cut without sp. change	-0.44	5.8	3.3	5	4.0	4.0	3
101	Uotila *et al.* (2005)	Plants	Lichens		10	50	Clear-cut without sp. change	0.28	5.0	0.8	4	5.7	3.1	3
102	Uotila *et al.* (2005)	Plants	Lichens		10	50	Clear-cut without sp. change	-0.63	5.3	2.1	4	3.3	3.2	3
103	Uotila & Kouki (2005)	Plants	Vascular		10	100	Clear-cut without sp. change	-0.33	19.5	4.4	4	18.0	2.7	3
104	Uotila & Kouki (2005)	Plants	Vascular		10	100	Clear-cut without sp. change	0.73	15.3	4.0	4	18.0	1.0	3
105	Uotila & Kouki (2005)	Plants	Vascular		10	100	Clear-cut without sp. change	0.67	11.8	5.4	9	15.3	1.2	3
106	Uotila & Kouki (2005)	Plants	Bryophytes		10	100	Clear-cut without sp. change	0.24	17.5	7.8	4	19.3	3.2	3
107	Uotila & Kouki (2005)	Plants	Bryophytes		10	100	Clear-cut without sp. change	-0.51	17.8	1.5	4	16.3	3.2	3
108	Uotila & Kouki (2005)	Plants	Bryophytes		10	100	Clear-cut without sp. change	-0.54	14.3	5.6	9	11.3	2.5	3
109	Uotila & Kouki (2005)	Plants	Lichens		10	100	Clear-cut without sp. change	0.99	2.8	1.9	4	4.7	1.2	3
110	Uotila & Kouki (2005)	Plants	Lichens		10	100	Clear-cut without sp. change	0.21	1.0	1.2	4	1.3	1.5	3
111	Uotila & Kouki (2005)	Plants	Lichens		10	100	Clear-cut without sp. change	-0.36	1.2	1.5	9	0.7	1.2	3
112	Vanbergen *et al.* (2005)	Animals	Arthropods	Carabids				1.06	8.3	2.7	16	12.0	4.0	16
113	Vanbergen *et al.* (2005)	Animals	Arthropods	Carabids				1.13	9.0	1.4	16	13.0	4.7	16
114	Vellak & Ingerpuu (2005)	Plants	Bryophytes				Selective cutting close-to-nature	-1.10	37.5	25.0	10	18.8	7.8	16
115	Vellak & Ingerpuu (2005)	Plants	Bryophytes				Selective cutting	-1.18	37.5	25.0	10	15.2	5.7	10
116	Vellak & Paal (1999)	Plants	Bryophytes		0.04			-0.02	1.5	0.6	115	1.5	1.1	79
117	Vellak & Paal (1999)	Plants	Bryophytes		0.04			-0.20	1.7	0.9	62	1.5	0.9	39
118	Vellak & Paal (1999)	Plants	Bryophytes		0.04			0.22	1.5	0.7	220	1.6	1.1	83
119	Winter *et al.* (2005)	Fungi				50		-0.80	80.0	11.7	2	74.0	3.9	5
120	Zach *et al.* (1999)	Animals	Arthropods	Coleoptera, Curculionidea		90	Selective cutting	0.86	12.0	6.0	10	20.0	11.1	10

TSA: Time since abandonment of management in unmanaged forests.

Hedges' *d*: Hedges' effect size for species richness between unmanaged and managed forests.

$\overline{X}^C$: mean species richness for the control (unmanaged) group; S^C : standard deviation of the control (unmanaged) group; N^C : sample size of the control (unmanaged) group; $\overline{X}^E$: mean species richness for the experimental (managed) group; N^E : sample size of the experimental (managed) group; S^E : standard deviation of the experimental (managed) group.

Appendix S3. References used for the meta-analysis.

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