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Review

Biodiversity Differences between Managed and Unmanaged Forests: Meta-Analysis of Species Richness in Europe

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Abstract: *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. The possible biodiversity gains and losses due to forest management (i.e., anthropogenic pressures related to direct forest resource use), however, 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 intensity 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,*

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lichens, fungi, 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. Clearcut forests in which the composition of tree species changed had the strongest effect on species richness, but the effects of different types of management on taxa could not be assessed in a robust way because of low numbers of replications in the management-intensity classes. Our results show that some taxa are more affected by forestry than others, but there is a need for research into poorly studied species groups in Europe and in particular 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.

Keywords: conservation policy, forest management abandonment, management intensity, meta-analysis, species richness, taxonomic diversity

Diferencias en la Biodiversidad entre Bosques Manejados y No Manejados: Meta-análisis de la Riqueza de Especies en Europa

Resumen: *Las presiones pasadas y presentes sobre los recursos forestales ha llevado a una disminución drástica de la superficie de bosques no manejados en Europa. Los cambios en la estructura, composición y dinámica de los bosques inevitablemente conduce a cambios en la biodiversidad de especies habitantes de bosques. Sin embargo, las posibles ganancias y pérdidas de biodiversidad debido al manejo de bosques (i.e., presiones antropogénicas relacionadas con el uso directo de los recursos forestales) nunca han sido evaluadas a escala paneuropea. Usamos meta-análisis para revisar 49 artículos publicados que contenían 120 comparaciones de la riqueza de especies entre bosques manejados y no manejados en Europa. Exploramos la respuesta de diferentes grupos taxonómicos y la variabilidad de su respuesta con respecto al tiempo desde el abandono y la intensidad del manejo del bosque. La riqueza de especies fue ligeramente mayor en bosques no manejados que en bosques manejados. Especies dependientes de la cobertura, continuidad, madera muerta y árboles grandes (briofitas, líquenes, hongos, escarabajos saprofílicos y carábidos) fueron afectadas negativamente por el manejo de bosque. En contraste, las especies de plantas vasculares fueron favorecidas. La respuesta de aves fue heterogénea y probablemente dependió más de factores como los patrones del paisaje. La diferencia global en la riqueza de especies entre bosques manejados y no manejados incrementó con el tiempo desde el abandono e indicó una recuperación gradual de la biodiversidad. Los bosques talados, en los que cambió la composición de especies de árboles, tuvieron el mayor efecto sobre la riqueza de especies, pero los efectos de diferentes tipos de manejo sobre los taxa no pudo ser evaluado de manera robusta debido al bajo número de replicaciones en las clases de intensidad de manejo. Nuestros resultados muestran que algunos taxa son más afectados por la silvicultura que otras, pero hay una necesidad de investigar grupos de especies poco estudiadas en Europa y en localidades particulares. Nuestro meta-análisis sustenta la necesidad de una red europea de investigación coordinada para estudiar y monitorear la biodiversidad de diferentes taxa en bosques manejados y no manejados.*

Palabras Clave: abandono de bosque manejado, diversidad taxonómica, intensidad de manejo, meta-análisis, política de conservación, riqueza de especies

Introduction

Almost all Europe's native forests have been altered by management of varying intensities (Vanbergen et al. 2005). Natural forests currently represent <1% of European forests, whereas 13% of forests on the west coast of the United States and 40–52% of forests in Canada are natural (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). Nevertheless, 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 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 dead wood and decaying trees, old and large trees, and pits and mounds around root plates (Peterken 1996; Hunter 1999; 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 but lack senescent phases (Kuuluvainen et al. 1996; Commarmot et al. 2005).

Nevertheless, there is still a debate over the global effect of forest management on biodiversity (Siitonen 2001). At the local scale, unmanaged forests in general are said to contain more species than managed forests (Okland et al. 2003). The results of some studies, however, failed to confirm this idea for particular taxa, such as vascular plants, birds, and soil invertebrates (Graae & Heskjaer 1997; Bobiec 1998), whereas results of other studies have showed 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). Thus, the literature does not systematically support the hypothesis that unmanaged forests are more species rich than managed forests. 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 within managed forests (Parviainen et al. 2000). This strategy relies on the assumption that lack of forest management may benefit many forest-dwelling species. Nevertheless, biodiversity recovery after cessation of forest management may be slow, and the benefits of setting up new forest reserves may not be detectable for some time. 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 accord with the assumption about the negative impact of forest management, one can assume that the more intense the management, the higher the difference in biodiversity between unmanaged and managed forests (e.g., Stephens & Wagner 2007).

We used meta-analysis to identify gaps in knowledge about the response of biodiversity to forest management in Europe. Although other reviews on the subject have been published, none used a meta-analysis (e.g., Niemelä et al. 2007; Stephens & Wagner 2007). We conducted this review to guide conservation policy that addresses forest biodiversity in unmanaged forests.

Treatment effects can be quantitatively analyzed with meta-analysis. The use of a common metric called effect size accounts for the fact that studies are not all equally reliable (e.g., studies with small sample sizes have lower statistical power than studies with large ones [Gurevitch et al. 2001]). Because effect size is not sample-size dependent, it allows comparison of 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 to obtain a relatively homogeneous sample in terms of biogeography and phylogeography. We used species richness as a surrogate for biodiversity because it is one of the simplest and most widely used indices of biological diversity (Noss 1990). Nevertheless, this approach can be misleading because it does not fully describe biodiversity (Magura et al. 2001; Standovar et al. 2006). We set out to answer the following questions: Is species richness systematically higher in unmanaged than in managed forests or does the effect of forest management vary widely with taxonomic and ecological group? For a given taxonomic or ecological group, does species richness change with time since abandonment, in line with a gradual recovery of the typical habitat conditions of unmanaged forests? And, for a given taxonomic or ecological group, does the difference in species richness between unmanaged and managed forests increase with management intensity?

Methods

Data Selection

We followed Pullin and Stewart's (2006) guidelines for systematic literature reviews (see Supporting Information). To be included in the analysis, a paper had to report summary data for species richness by comparing managed versus unmanaged treatments. We selected 49 papers published between 1978 and 2007 (Table 1). These publications contained 120 comparisons (hereafter referred to as individual studies; Supporting Information). Unpublished material and grey literature were not included in the data set.

In the selected papers, the term *forest management* meant any anthropogenic pressures related to direct use of forest resources (thinning, clearfelling, selective felling, any form of tree retention, grazing, and planting) (Table 1). We did not consider human impacts such as pollution, eutrophication, climate change, or other indirect pressures. Most of the forests considered 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*, *subnatural*; sensu Peterken 1996) were also included.

The individual studies that compared mature forests with a young regeneration phase or clearfellings were excluded because these early short-term phases are very different from older phases, regardless of whether or not they are managed. Nevertheless, individual studies were included in the analysis if similarly managed and unmanaged successional phases following natural disturbances were compared (e.g., young managed vs. young unmanaged, old managed vs. old unmanaged).We used species

Table 1. Structure of the data set (individual studies) used to compare the species richness in managed and unmanaged forests[a]

	Management type					*Biome*		
Taxa	*clearcut with species change[e]*	*clearcut without species change[f]*	*selective felling[g]*	*selective felling close to nature[h]*	*UD[i]*	*boreal*	*temperate*	*Total*
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[b]	4	7	10	3	4	12	16	28
Vascular[b] & bryophytes			1				1	1
Animals	8	12	15	6	11	36	16	52
Acari oribatids					3		3	3
All arthropods[c]		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
Nonsaproxylic beetles	1	5	1	1		8		8
Saproxylic beetles[d]	1	5	6	2	3	17		17
Fungi			6	5	1	11	1	12

[a] *the table includes all the studies referenced in the bibliographic review. Some groups were not analyzed because they included only one comparison or were from only one study, i.e.: vascular plants and bryophytes, all arthropods together, Acari oribatids, Araneae, Curculionidea.*
[b] *Includes ferns.*
[c] *this group derives from studies without taxonomic distinction within the group.*
[d] *Includes bark beetles.*
[e] *clear-cut forests with tree species change.*
[f] *clear-cut forests without tree species change, including natural regeneration and plantations without species change.*
[g] *forests managed by selective felling (continuous cover), without reference to "close-to-nature" management.*
[h] *forest managed by selective felling with reference to "close-to-nature" management.*
[i] *undetermined type.*

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 (Supporting Information). We extracted data from the text, tables, and graphs. The Hedges' *d* effect size defines the standardized difference between mean species richness of managed forests (experimental group, $\bar{x}^E$) and unmanaged forests (control group, $\bar{x}^C$) divided by the pooled SD (S) and multiplied by a correction factor (J):

$$d = J\,\frac{\bar{x}^E - \bar{x}^C}{S}, \tag{1}$$

$$S = \sqrt{\frac{(N^E - 1)(S^E)^2 + (N^C - 1)(S^C)^2}{N^E + N^C - 2}}, \tag{2}$$

and

$$J = 1 - \frac{3}{4(N^C + N^E - 2) - 1}, \tag{3}$$

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

A negative *d* value means higher species richness in unmanaged than in managed forests. We combined effect sizes across all studies to provide the grand mean effect size (d_{++}) (Gurevitch & Hedges 1999). We also calculated the log response ratio ($\ln R = \frac{\ln(\bar{x}^E)}{\ln(\bar{x}^C)}$), which gives an estimate of the percentage of variation in species richness between managed and unmanaged forests. Following Pullin and Stewart (2006), we opted for random-effects models rather than fixed-effects models because 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 (CI), calculated with 999 iterations, did not bracket zero. We checked the entire data set and the three data subsets (plants, animals, and fungi) for publication bias with Spearman rank-order correlation (effect vs. variance). This test accounts for the fact that nonsignificant 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 CI 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: saproxylic beetles (species that depend on deadwood during some part of their life cycle [Speight 1989]) and nonsaproxylic beetles. Because we expected heterogeneous results for higher taxonomic levels (e.g., kingdom), we analyzed only elementary groups if they contained at least two individual studies (Table 1). We used a random-effects model to calculate an effect size (d_+) for each taxonomic group. We tested the total heterogeneity Q_T of each group against a chi-square distribution and considered the group 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 with a continuous random-effects model and a log transformation for plot area. For each study, we then tabulated time since abandonment (TSA) of management in the unmanaged forest when available, and analyzed the global response and the response for each taxon with a continuous random-effects model. We did not include studies devoid of TSA information in this analysis. We also defined four classes of management types (ranked in the following in decreasing order of management intensity): (1) clearcut with species change, clearcut forests with tree species composition change (native and non-native species); (2) clearcut without species change, clearcut forests without tree species change, including natural regeneration and plantations without species change; (3) selective felling, forests managed by selective felling (continuous cover) without reference to close-to-nature management; (4) selective felling close-to-nature management, 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 was a factor in only one article (Hansson 2001), and it was not included in the analysis. We analyzed the global response and the response of each taxonomic group with mixed-effects models. The significance of the mean effect size for a taxonomic group (d_+) was tested by calculating a 95% bootstrap CI (999 iterations). The effect was considered significant if the 95% bootstrap CI did not bracket zero. We explored variation in effect sizes across management types by calculating between-class heterogeneity (Q_B) and testing the result 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. We used MetaWin 2.1 software (Rosenberg et al. 2000) for the meta-analysis.

Results

General Data Structure and Publication Bias

Our data set contained 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 12 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.

The TSA varied from 10 to 160 years for 89 studies. Twenty-three studies, mainly located in the boreal zone, referred to old-growth stands, but did not provide precise TSA.

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

Spearman's rank correlation of the entire data set was not significant ($R_s = -0.006, p = 0.945$), which indicated no publication bias. Publication bias for plants, animals, and fungi was also not significant (plants: $R_s = 0.121$, $p = 0.376$; animals: $R_s = -0.036, p = 0.802$; fungi: $R_s = -0.168, p = 0.602$).

Meta-Analysis

Species richness was higher in unmanaged than in managed forests, as indicated by the negative grand mean calculated for the entire data set (Table 2 & Fig. 1). The effect, however, was only marginally significant (the upper boundary of bootstrap CI 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, which indicated 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 (Cohen 1969). The calculation of the log response ratio showed variation percentages from -30% to $+13\%$ (Table 2). Vascular plants and nonsaproxylic beetles showed indications of higher species richness in managed forests, but the result was only marginally significant for vascular plants and was not significant for nonsaproxylic 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, whereas other groups (birds, all

Table 2. Effect of forest management on total species richness and species richness of different taxonomic groups in European forests[a]

Taxa	*Average* d d_+ *or* d_{++}	*Bootstrap CI* −	+	n	Q_T	$p(Q_T)$	*Variation (%)*
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
Nonsaproxylic 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

[a] *One study gave the Shannon index in place of species richness but was included anyway (Vellak & Paal 1999, see Supporting Information). Average* d*, Hedges'* d *effect size;* d_{++}*, grand mean;* d_+*, 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 tested against a chi-square distribution; variation, difference in species number between managed and unmanaged forests expressed as a percentage calculated with the log response ratio; *, marginally significant effect and significant effect.*
[b] *Includes ferns.*
[c] *Includes bark beetles.*

arthropods, acari oribatids) yielded nonsignificant results. Total heterogeneity (Q_T) was never significant.

For plot-area effect on vascular plants, we analyzed 21 individual studies (out of the 28 available). Census plot area for vascular plants ranged from 4 m^2 to 400 m^2. There was no significant effect of plot area on effect size ($p = 0.11$).

For effect of TSA, 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 (Fig. 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 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 because the intercept was negative.

We analyzed the effect of management type in 100 individual studies. When all taxa were included, mean effect sizes differed marginally among the management types (Table 4). "Clearcut 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 "clearcut without species change" type, but was slightly negatively affected in the "selective felling" and "selective felling close-to-nature" types.

When the data set was divided into taxonomic groups, only bryophytes and lichens showed significant differences among management types: "selective felling"

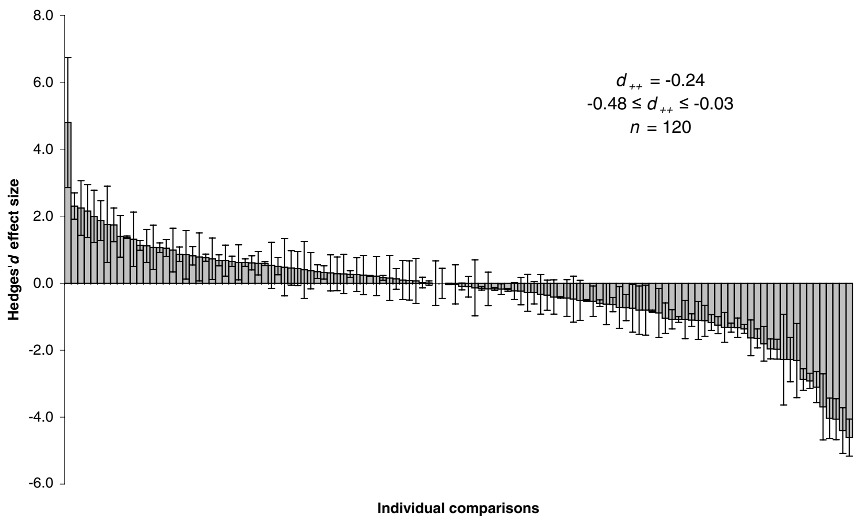

Figure 1. Hedges' d *effect size and variance (error bars) of individual studies in a comparison of species richness between unmanaged and managed forests. A negative effect size means species richness was higher in unmanaged forests than in managed forests. More information on each study is in Supporting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

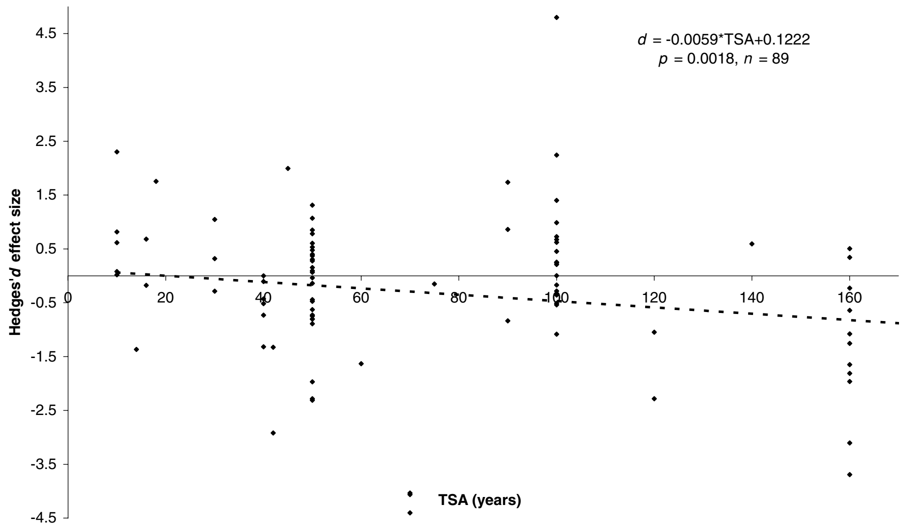

Figure 2. Regression plot of the effect of time since abandonment (TSA) of management in the unmanaged forests on Hedges' d *effect size. The TSA effect was analyzed with a continuous random-effects model; Probability (*p*) was tested against a normal distribution (*n*, number of individual studies). See Table 3 for details.*

and "selective felling close-to-nature" significantly decreased the species richness of bryophytes and "selective felling" significantly decreased the species richness of lichens. For all the other groups, there were no significant differences among management types. Nevertheless, these results had a low statistical power because of the limited number of individual studies in each type.

Table 3. Response to forest management of each taxonomic group with respect to time since abandonment (TSA)[a]

Taxa	*Intercept (SE)*	*Slope (SE)*	p	n	*TSA range (minimum–maximum)*
All	0.122 (0.215)	−0.0059 (0.0025)	0.0018	89	10–160
Vascular plants[b]	0.762 (0.319)	−0.0037 (0.0046)	0.43	23	10–140
Bryophytes	−0.546 (0.527)	0.0057 (0.0084)	0.50	8	14–100
Lichens	0.436 (0.917)	−0.0083 (0.0086)	0.39	10	50–120
Birds	−0.728 (0.467)	0.0063 (0.0070)	0.37	7	30–100
Carabids	1.393 (0.478)	−0.0782 (0.0027)	0.004	6	42–70
Saproxylic beetles[c]	−0.200 (0.448)	−0.0094 (0.0041)	0.02	12	40–160
Nonsaproxylic beetles	1.156 (0.738)	−0.0098 (0.0061)	0.11	6	50–160
Fungi	0.872 (0.597)	−0.0202 (0.0071)	0.005	11	50–160

[a] *The TSA effect was analyzed with a continuous random-effects model. Probability (*p*) was tested against a normal distribution (*n*, number of individual studies).*
[b] *Includes ferns.*
[c] *Includes bark beetles.*

Table 4. Response to forest management of each taxonomic group with respect to management intensity[a]

	Clearcut with species change		*Clearcut without species change*		*Selective felling*		*Selective felling close to nature*			
Taxa	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[b]	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[c]			−0.36	5	−1.14*	6	−1.27*	2	1.53	0.465
Fungi					−0.44	6	−0.97*	5	0.67	0.412

[a] *Groups included in these analyses contained at least two individual studies in each management intensity class (*d_+*, Hedges'* d *effect size for each management intensity class;* n*, number of individual comparisons;* Q_B*, between-group heterogeneity;* $p(Q_B)$*, heterogeneity tested against a chi-square distribution; *, significant effect; **, marginally significant effect.*
[b] *Includes ferns.*
[c] *Includes bark beetles.*

Discussion

Taxonomic Groups' Contrasting Responses to Forest Management

Our 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 (+6.8%), but the response varied widely among taxonomic groups.

Several mechanisms may explain the effect of management on forest biodiversity: changes in tree age structure, vertical stratification, and composition of tree species, which affect light, temperature, moisture, litter, and topsoil conditions (Sebastia et al. 2005; Standovar et al. 2006); presence of microhabitats (e.g., dead wood, veteran trees, cavities, root plates) specific to unmanaged (Berg et al. 1994; Bouget 2005*a*; Christensen et al. 2005; Gibb et al. 2005) or managed forests (e.g., skid trails and haul roads) (Hansen et al. 1991; Gosselin 2004); and 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 significant higher species richness in unmanaged forests. These substrate-dependent taxa suffer from reduction of microhabitat availability and diversity in managed forests. The quantitative and qualitative features of dead wood, the presence of large logs and snags, and the presence of different decay stages are the key elements for these taxa (Bouget 2005*b*; Odor et al. 2006; Hjalten et al. 2007; Johansson et al. 2007). Fine-scale soil disturbances under natural forest-stand dynamics (e.g., establishment of pits, mounds, and root plates) considerably increased the diversity of several taxa, such as bryophytes and lichens (Jonsson & Esseen 1990; Kimmerer 2005). Additionally, microhabitat continuity is especially important for dispersal-limited groups that are favored by stable conditions (e.g., 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). 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 understory vascular plants, especially shade intolerant, ruderal, and competitive species, but they can also favor shade-tolerant and stress-tolerant species (Brunet et al. 1996; Schmidt 2005). This generally results in an increase in total species richness. Nevertheless, stand age, relative to natural forest dynamics, may also influence the species richness of vascular plants.

Changes in Forest Management Effect over Time

Time since abandonment in unmanaged forests significantly influenced effect size. In the first 20 years, species richness was higher in managed than unmanaged forests; 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 unmanaged have 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 microhabitats in unmanaged forests can increase species richness. Other substrate-dependent groups such as lichens and bryophytes, however, 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 recolonization of species dependent on typical unmanaged forest substrates.

Nevertheless, 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. Recolonization by forest specialists can be difficult even if the stand is left unmanaged for a long time. For example, dispersal limitation is 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 dead wood discontinuity may explain the absence of dispersal-limited epixylic bryophytes, which need relatively long intervals to recolonize the younger reserves (Odor et al. 2006).

Effect of Management Intensity

We expected that the more intense forest management was, the higher the species richness difference between unmanaged and managed forests would be. Our results showed that the effect of forest management varied with management intensity. In comparison with the unmanaged reference, the strongest difference in species richness was observed for forests that underwent clearcutting and changes in tree species in the past (Stephens & Wagner 2007). Conversely, species richness of forests clearcut in the past but that did not undergo a change in tree species (natural or artificial regeneration) did not differ from unmanaged references. Clearcutting is typical in boreal forests because it mimics the natural fire-disturbance regime. Clearcutting, however, may strongly diverge 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 management 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 because of the low number of replications in each class. It was also impossible to test the interaction between management type and TSA, but even if it had been testable, it would still have raised the problem of low replication number.

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

Possible Confounding Effects and Meta-Analysis Limitations

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, because forest management per se influences tree composition and stand age or succession, we considered that these factors did not have to be controlled systematically.

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 we analyzed rarely adopted a sampling design on the basis of 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 four individual studies controlled landscape). The effect of adjacent landscape structure could override the forest management effect, especially for mobile groups such as birds and carabids, because the population dynamics of many organisms operate at larger scales than a forest stand (Helle 1986; Magura et al. 2000; Brotons et al. 2003; Lohmus 2004). Compared with managed forests, most of the unmanaged patches are probably too small to be considered 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 of 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 decreased availability of nesting and feeding habitats (Lohmus 2004). In addition, recent research underlines 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 of our meta-analysis is its reliance on the use of plot-level species richness as a surrogate for biodiversity. 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 (Kolb & Diekmann 2005; Johansson et al. 2007; Bernhardt-Romermann et al. 2008) (i.e., herbivorous vs. predators or saproxylic vs. nonsaproxylic 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]). Nevertheless, 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. One would need the original data set of each study (i.e., plot–species matrix) to conduct such an analysis.

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 detection of an effect of plot area would have implied that differences in species richness were scale dependent. Because forest is a mosaic of dynamic ecosystems (Spies & Turner 1999), the alpha-diversity index we considered was an incomplete descriptor of the management effect; it would have been better to compare alpha, beta, and gamma diversity between managed and unmanaged forest landscapes. For example, results of plant-community studies show that unmanaged forests display higher beta diversity of plant communities because of higher within-stand habitat heterogeneity (Bobiec 1998) and that observed differences between unmanaged and managed sites are strongly dependent on spatial scale (Standovar et al. 2006).

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, or did not report species richness summary data. In addition, many studies dealt with other descriptors of biodiversity than species richness, such as biomass (ungulates: Jedrzejewska et al. 1994), number of pairs per area unit (birds: Kouki & Vaananen 2000; Virkkala & Rajasarkka 2006), or abundance or species composition (insects: Vaisanen et al. 1993; Simila et al. 2003). Another critical problem in the literature selection was the relatively scant reporting of summary statistics (SD and n) not only in old, but also in recent publications. This problem has 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-analyses. 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 depended closely on the selection criteria, we discovered a critical knowledge gap concerning several important taxa in Europe. There were few reports on arachnids, mollusks, and soil fauna 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, census plot area, habitat size and other landscape structure patterns, and past land-use and management history because it is important to control the influence of these possible confounding factors in sampling strategies. We emphasize the need to analyze the response of species composition to forest management and to use functional classifications to determine which species traits are 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. Our results also show that the time of abandonment needed for the biodiversity to recover ranges from 0 to >40 years, depending on the taxa. Although our results have to be confirmed by complementary studies, we emphasize that the time required for recovery of the biodiversity in unmanaged forests may prove particularly long for several groups, which means the efficiency of conservation policy needs to be assessed within a long-term perspective.

Forest conservation priority should focus on saproxylic beetles, bryophytes, lichens, carabids, and fungi because these taxa proved the most sensitive to forest management. Nevertheless, other taxonomic groups also need to be monitored because there were few studies available on these groups for our meta-analysis. More generally, because different taxa responded differently to forest management, the conservation priority should be taxa whose habitats are most threatened by forest management (e.g., dead wood, infrequently disturbed areas).

We strongly support creation of a coordinated monitoring network to compare biodiversity between unmanaged and managed forests (Parviainen et al. 2000; Larsson 2001; Meyer 2005). This kind of network would provide basic information, such as species richness for several taxonomic groups, and more fundamental knowledge on the patterns and processes involved in forest biodiversity.

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Supporting Information

Bibliographic review method and English keywords used for database searches (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. 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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