REVIEW

Effects of land use on plant diversity – A global meta-analysis

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Summary

1. Plant diversity is globally threatened by anthropogenic land use including management and modification of the natural environment. At regional and local scales, numerous studies world-wide have examined land use and its effects on plant diversity, but evidence for declining species diversity is mixed. This is because, first, land use comes in many variations, hampering comparisons of studies. Second, land use directly affects the environment, but indirect effects extend beyond the boundaries of the land in use. Third, land-use effects greatly depend on the environmental, historical and socio-economic context.

2. To evaluate the generality and variation of studies' findings about land-use effects, we undertook a quantitative synthesis using meta-analytic techniques.

3. Using 572 effect sizes from 375 studies distributed globally relating to 11 classes of land use, we found that direct and indirect effects of land use on plant diversity (measured as species richness) are variable and can lead to both local decreases and increases. Further, we found evidence (best AIC model) that land-use-specific covariables mostly determine effect-size variation and that in general land-use effects differ between biomes.

4. *Synthesis and applications*. This extensive synthesis provides the most comprehensive and quantitative overview to date about the effects of the most widespread and relevant land-use options on plant diversity and their covariables. We found important covariables of specific land-use classes but little evidence that land-use effects can be generally explained by their environmental and socio-economic context. We also found a strong regional bias in the number of studies (i.e. more studies from Europe and North America) and highlight the need for an overarching and consistent land-use classification scheme. Thereby, our study provides a new vantage point for future research directions.

Key-words: diversity, effects, land management, land use, meta-analysis, plants, species richness

Introduction

Plant diversity is instrumental to ecosystem health and human well-being (Daily 1997; Quijas, Schmid & Balvanera 2010; Cardinale *et al.* 2011; Isbell *et al.* 2011; De Mazancourt *et al.* 2013). While plant diversity is globally threatened by anthropogenic ecosystem degradation and land use (Vitousek *et al.* 1997; Sala *et al.* 2000), various effects at regional to local scale have been reported (e.g. Vellend *et al.* 2013; Murphy & Romanuk 2014). In part, land use directly changes ecosystems via land modification, fragmentation and intensification (Lambin & Geist 2006), but land use also indirectly affects habitat characteristics linked to species diversity, such as area, edges

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and age, not only of the managed land but also of remaining natural land within the same matrix. Sustainable land use is required to sustain ecosystem health in the long term, balancing human needs and ecosystem functioning. Therefore, quantitative knowledge about the effects of land use on ecosystem responses such as species diversity is highly relevant (DeFries, Foley & Asner 2004).

To date, numerous studies world-wide have examined various types of land use and its effects on plant diversity, mostly conducted at local to regional scales (scale of inference from 10^{-2} to 10^{9} m²). These studies report various effects depending on the considered land use and reference state. A commonly used tool to evaluate such variation in study findings and to generalize conclusions is meta-analysis (e.g. Arnqvist & Wooster 1995). Meta-analyses are able to detect the direction, magnitude and variability of effect sizes, which is important for determining relevant covariables, and why meta-analyses are gaining increasing popularity in ecology (Cadotte, Mehrkens & Menge 2012). Specifically, effects of land use might depend on land-use-specific covariables and more generally on the environmental, historical and socio-economic context.

Several meta-analyses investigating sets of possible land-use effects on biodiversity have been published (cf. Appendix S1 in Supporting Information for a summary). While these reviews make important contributions to our understanding of land-use effects on diversity, they lack direct comparability due to different land-use types, taxa, responses, effect-size measures or regional constraints. We aim at filling this gap by conducting a comprehensive meta-analysis (*sensu* Vetter, Rücker & Storch 2013) that allows for a global comparison of multiple land-use types at once while focussing on plant species richness.

We considered land use that involves management within and transitions between the five land-cover states: agroforest, forest, pasture, cropland and grassland (cf.

Fig. 1, Table 1). Transition within land-cover states encompasses intensification but also fire management. Additionally, we included patch area (linked to fragmentation), habitat age (linked to abandonment or duration of management) and edge effects (linked to matrix effects), which are more indirectly but undoubtedly related to land-use impacts. Moreover, land-use effects extend beyond the boundaries of transformed land in that land use affects untransformed habitat in the same matrix as well, for example by decreasing patch area or affecting habitat edges.

Using an extensive data set extracted from published studies, we have asked the following questions: (i) What is the direction and magnitude of effects of a large set of land-use options on plant species richness world-wide? (ii) How important are land-use-specific covariables and study-specific covariables such as study design, spatial scale, and the environmental, historical and socio-economic context for explaining effect-size variation? (iii) How do effects vary within land-use classes and considering the most important covariables according to (ii)?

We guided our analysis of the varying effects of different land-use options using hypotheses for land-use-specific effects and selected land-use-specific covariables, grounded in ecological theory of patterns and mechanisms of plant diversity (e.g. Tilman & Pacala 1993). (i) Moderate disturbance is favourable for species richness (Tilman 1982); hence, we hypothesized that grassland and forest management (such as silviculture and agroforestry) as well as moderate fire regimes, which generate conditions favouring fire-adapted species otherwise absent from unburned vegetation (Tilman 1982), lead to overall positive effects. We hypothesized that prescribed fires are less intense than wildfires and therefore show a higher positive effect than wildfires. In contrast, high-disturbance land use implies land-cover transitions (such as deforestation or cropland expansion) and should cause overall negative effects.
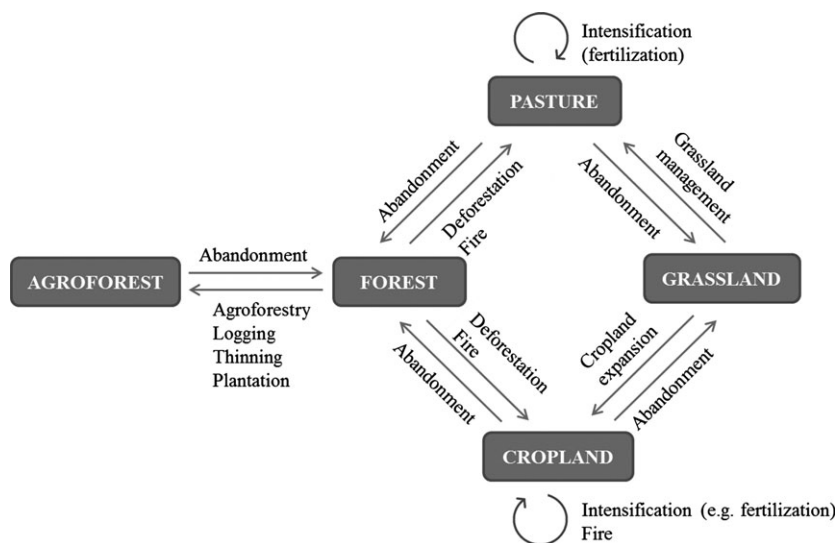

Fig. 1. Typical transitions between land-cover states and intensification (figure inspired by Lambin & Geist 2006).

Table 1. Land-use classes considered and their definitions used in the meta-analysis. Left column indicates whether land-use classes directly or indirectly affect the environment

Direct	
Abandonment	Long-term abandonment (more than 8 years) from active management (e.g. agriculture, grassland management, silviculture, plantation)
Agroforestry	Combining trees and shrubs with crops and/or livestock
Deforestation	Cutting forest in order to establish pastures or cropland on that land
Fertilization	Nutrient input (with N or P) or organic (control) vs. conventional (managed) farming
Fire	Prescribed or naturally occurring fire
Grassland management	Grazing (of large herbivores) or mowing several times per year. Only studies using climax natural grasslands or short-term exclosures (less than 8 years) were considered. In contrast, long-term exclosures (more than 8 years) where succession has already started were classified as abandonment
Plantation	Artificially established forest, farm or estate, where crops are grown for sale
Silviculture	Logging (large-scale cutting of forest including clear cutting) or thinning (reducing basal area of a forest)
Indirect	
Edge effects	For managed patches, the land-use intensity gradient follows the distance gradient from the edge towards the centre. For natural patches next to managed patches, this gradient is reversed, that is, from the centre towards the edge. Edge effects are linked to fragmentation and land-use expansion.
Habitat age	Duration of management or temporal proximity to last disturbance (agricultural or silvicultural management, fire) or habitat establishment (successional stage), all consider different stages of the same treatment (in contrast to abandonment)
Patch area	Increase in patch area of managed land or decrease in patch area of remaining natural land

(ii) Intensification of land use through fertilization should cause a decline of species richness, because high amounts of nutrients only favour single species, which then dominate the community (Bobbink *et al.* 2010). Dominant species should also be responsible for lower species richness in monoculture plantations, where light availability is decreased for species in the understorey, but it has been found that effects depend on the initial land cover (Bremer & Farley 2010; Felton *et al.* 2010); the effects might even be positive, for example in cases where plantations replace agroecosystems. (iii) Specific effects of abandonment of active management might depend on the management itself (e.g. severity and time since last disturbance; Pickett, Collins & Armesto 1987). We hypothesized that effects of abandonment are mainly the opposite compared to the effects of the previous management. For example, while abandoning plantations and croplands might be positive, abandoning forest and grassland management may cause a decline in species richness. (iv) Land-use intensification is often accompanied by land-use expansion, that is, managed patch area increases at the expense of decreasing area of remaining natural land. We hypothesized that increasing patch area of managed land is positively associated with species richness for managed land due to the species–area relationship (Rosenzweig 1995) but reduces species richness in the remaining natural land. Moreover, since managed patches tend to be more homogenous than natural patches, we expected a lower increase in species richness with area and hence lower absolute effects of increasing patch area for managed land compared to natural land. (v) Theory of plant succession predicts an initial increase in plant diversity and after a peak a much slower decrease (Huston & Smith 1987). Hence, we hypothesized that in general habitat age in abandoned/unmanaged patches (subject to suc-

cession) shows positive effects, while in managed patches succession is suppressed and might not have a significant effect. (vi) Edge effects were defined as the correlation between species richness and distance from the edge for managed patches and distance from the centre for natural patches and therefore should differ between natural and managed patches. Particularly, we hypothesized that edge effects in managed patches are negative since species spill over (Blitzer *et al.* 2012) from neighbouring natural patches, but management restricts coexistence of species in the centre of managed patches (Ries *et al.* 2004).

We selected study-specific covariables, that is, covariables of land use that are supposed to explain effect-size variation across the range of land-use classes: we considered spatial scale using plot size, that is, the area for which species richness was compared, since it has been suggested that effect sizes are scale dependent and depend on species pool size (Chase & Knight 2013). Additionally, we included biotic or abiotic conditions reflecting the environment and evolutionary history (biomes or climatic regions), which both determine species pool size (Blackburn & Gaston 2003). Species pool size is also affected by land-use history (Peterken & Game 1984; Bruun *et al.* 2001). To this end, we included short-term (initial land cover or land-use system) and long-term historical context (continents as a proxy of land-use history, Ellis *et al.* 2013). Furthermore, we explored the importance of socio-economic regions (country and economic region), which might determine land-use practices (e.g. fertilization or logging intensity). Finally, we included study design (i.e. experimental or observational), since both study types are likely to differ in the spatial scales used to make inferences and the degree of site similarity (Fortin & Dale 2005). For example, experimental studies usually aim at controlling site characteristics, that is, ensuring higher similarity between sites.

Materials and methods

STUDY SELECTION AND DATA EXTRACTION

We conducted a literature search following a hierarchical procedure. First, we used a title search in Web of Science (cf. Appendix S1, Supporting information for search terms). This revealed 1187 studies (on 28 June 2011). In a second step, we searched for meta-analyses and systematic reviews on land-use effects using Web of Science and Google search (Appendix S1, Supporting information). We explored references to studies examining land-use effects on plants and matching the criteria for inclusion. We also took into account studies cited in the papers obtained through the first selection step that matched some of the keywords in the title.

We designated studies as relevant if several criteria in form, content and method were matched, following hierarchical criteria:
 1. We only included peer-reviewed primary literature written in English. Hence, we excluded unpublished articles, articles not written in English and review papers.
 2. Studies had to investigate plant diversity in terms of species richness as a response variable and one of the predefined land-use classes (cf. Fig. 1, Table 1) for comparison.
 3. Studies must have a sufficient sample size and provide sufficient statistics for evaluation (see Statistical methods).

In total, 375 studies distributed world-wide (Fig. 2) matched these criteria, providing 572 effect sizes (due to multiple reported effects per study) and variances for the statistical analysis (Appendix S2, Supporting information).

Land-use classes were assigned using the classification scheme in Table 1, Fig. 1. While the majority of these classes are direct outcomes of land-use decisions, others are rather indirectly linked, such as habitat age, edge effects and patch area. These are linked to fragmentation and land-use expansion, which can be considered a side product of land-use decisions. We collected covariables related to our hypotheses, particularly whether fire was natural or prescribed, which land use was abandoned and whether patch area, habitat age and edge effects were studied in natural or managed patches.

To investigate systematic variation of land-use effects, we collected a set of parameters (see Appendix S3, Supporting information for details) relating to biotic conditions (the corresponding biome: Olson *et al.* 2001), abiotic conditions (the corresponding climatic region: Köppen-Geiger Classification: Kottek *et al.* 2006), short-term historical context (initial land cover: HYDE 2.0 classification: Goldewijk 2001) and initial land-use system (grassland, agroecosystem, forest or agroforest) and the long-term historical context (continent). We further coded socio-economic covariables (country and economic region: Lotze-Campen *et al.* 2008). Categorical variables, unless directly stated in the study itself, were assigned to the prevailing class in the study area determined using ArcGIS (ESRI 2011). Further, we coded how evidence was obtained (observational or experimental study design) and plot size (area for which species richness was compared). We categorized plot size into three levels: small (0.01–10 m²), intermediate (10–10^3 m²) and large (10^3–10^9 m²).

STATISTICAL METHODS

As a measure of effect size, we used Fishers' z-transformed correlation:

$$z = 0.5 \cdot \ln((1 + r)/(1 - r)), \mathrm{var}(z) = 1/(n - 3), \qquad \text{eqn 1}$$

where n is the sample size and r denotes the correlation coefficient between land-use intensity and species richness (Borenstein *et al.* 2009). We inverted the sign of the correlation in the case of abandonment, where recently abandoned patches were compared to patches still managed. For the indirect effects of patch area, habitat age and edge effects, we defined higher land-use intensity depending on whether managed or natural patches were considered: more intensive land use often implies an increase in patch area of managed land and thereby a decrease in patch area of remaining natural land. Similarly, we assumed an intensity gradient from the edge towards the centre of managed land, but from the centre towards the edge for neighbouring natural land. In case of habitat age, longer duration of management and temporal proximity to the last management/disturbance event in cases of unmanaged land indicate higher land-use intensity.

An effect size of zero indicates no effect, whereas positive effect sizes indicate an increase in species richness with land-use intensity. Similarly, negative effect sizes indicate a decrease in species richness with land-use intensity. When using correlation coefficients as effect size, the absolute magnitude indicates the strength of the effect but does not have an ecological interpretation in terms of how many species are lost or gained.

To estimate effect sizes from studies, we required means of species richness and standard error of the means within plots of different treatments, F-statistics or t-statistics from a one-way ANOVA, Pearson or Spearman rank correlation coefficients (directly reported or calculated from raw data), or P-values with corresponding statistics. For studies comparing only two groups, we first calculated standardized mean differences and transformed them to correlation coefficients (cf. Borenstein *et al.* 2009).

Some studies reported multiple outcomes, for example contrasted multiple land-use classes to a common control or multiple
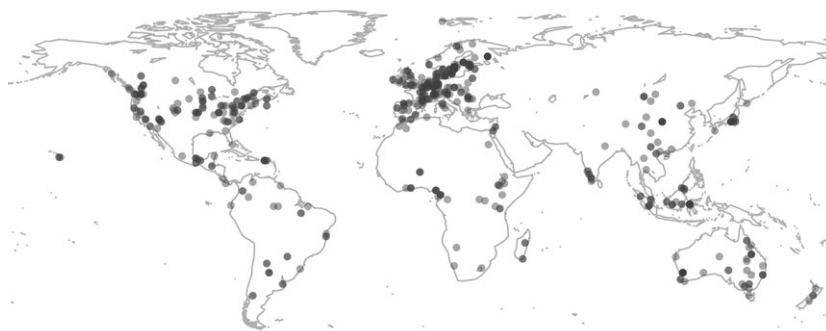
Fig. 2. World map showing the distribution of study sites. There is evidence for bias towards Europe and North America where 40.3% and 28% of studies were conducted. The majority of countries (73.5%) are not represented in the data base.

controls to a common land-use class, or reported contrasts for several subgroups of plants. Thus, contrasts within a study were not independent. We accounted for such non-independence by including a study-level random effect (Nakagawa & Santos 2012).

We used the inverse of variances to calculate study weights, thus giving more importance to studies with higher sampling effort (cf. equation 1). To avoid unequal weighting of studies with one versus more outcomes, we adjusted study weights (i.e. the inverse variance of effect sizes) by calculating the mean variance $\bar{v}$ within a study j and multiplying by the number k_j of outcomes reported in that study (following Hedges, Tipton & Johnson 2010). Hence, the weight for the ith effect size corresponding to study j was calculated as:

$$w_{ij} = \frac{1}{k_j \bar{v}_{.j}} = \frac{1}{\sum_{i=1}^{k_j} v_{ij}}, \qquad \text{eqn 2}$$

We analysed variation of effect sizes using linear mixed-effects models (R version 3.0.1: R Core Team 2013; function 'lme', package 'nlme': Pinheiro *et al.* 2013). This function particularly enables the user to specify weights and thus is suitable for performing multilevel meta-analyses (Nakagawa & Santos 2012). In order to estimate land-use-specific effect sizes, we fit a model using study as random effect and land-use class as fixed effect (hereafter land-use-only model). We compared mean effect sizes and their 95% confidence intervals (CIs). Conservatively, we considered effect sizes significant if the corresponding 95% CI did not cover zero and significantly different from each other if the corresponding 95% CIs did not overlap. We analysed the effects of land-use-specific covariables such as wildfire vs. prescribed fire, the role of initial land-use systems for plantations, patch area and edge effects on natural vs. managed patches, and habitat age of managed vs. abandoned land subject to succession. Further, to explore the importance of general land-use covariables, we included plot size, biomes, climatic regions, initial land cover, initial land-use systems, continents, countries, economic regions and study design and tested for additive effects and interactions with land use. To rank the relative importance of covariables, we compared models by Akaike information criterion (AIC, Burnham & Anderson 2002) and reported ΔAIC (the difference between a specific model's AIC and the minimum AIC relating to the best model) and AIC weights (Burnham & Anderson 2002). Further, we calculated a coefficient of determination R^2 for linear mixed-effects models (Nakagawa & Schielzeth 2013). We checked the model assumptions by visually checking the residuals for homogeneity and approximate normality of the standardized residuals using a Q-Q plot but did not find any violations of model assumptions.

Any kind of literature synthesis is prone to bias (Gurevitch & Hedges 1999; Nakagawa & Santos 2012). Publication bias describes the tendency that significant findings are more likely to be published (Gurevitch & Hedges 1999; Nakagawa & Santos 2012). However, the detection of publication bias can be caused by several factors, for example by real heterogeneity between effect sizes, which can be accounted for by covariables (Nakagawa & Santos 2012). Therefore, we tested several models for publication bias. To account for variation explained by the models, we plotted standard errors of effect sizes against the model residuals and tested for publication bias using Egger's regression (Egger *et al.* 1997; Nakagawa & Santos 2012):

$$y_i \sqrt{w_i} = \beta_o + \beta_1 \sqrt{w_i} + \varepsilon_i, \varepsilon_i \sim N(0, \sigma^2) \qquad \text{eqn 3}$$

where y_i is the ith residual and w_i is the ith weight. Publication bias was evident if the intercept is significantly different from zero.

Results

We found mostly negative effects of land use on plant species richness, but the strength and direction of the relationship varied depending on study characteristics. Exploring the importance of covariables in determining variation of effect sizes, the most parsimonious models considered land-use-specific covariables alone and in addition to plot size, and the model considering additive effects of land use and biomes (see Table 2 for the six best models, Table S1 in Appendix S4, Supporting information for all models). These models had an AIC weight of 0·728, 0·199 and 0·072, respectively. All models explained approximately equal amounts of effect-size variation, with R^2 ranging between 0·281 and 0·288. Plot size was of minor importance. The model accounting for both land-use-specific covariables and plot size was inferior (in AIC) to the land-use-by-covariables model. The land-use-only model was ranked at eighth place, explaining only 17·6% of between-study variability, and was rather poorly supported by our data (in terms of AIC weight; Table S1 in Appendix S4, Supporting information).

To study how effects vary within land-use classes, and considering the most important covariables according to our model ranking, we now present results from (i) the land-use-only model (Fig. 3), (ii) the land-use-by-covariables model (covariables specific to land use where appropriate) (Fig. 4) and (iii) the land use + biome model (Fig. 5). Most of our hypotheses regarding the direction of land-use effects were confirmed, that is, we detected significant positive effects of silvicultural management, such as logging and thinning, and significant negative effects of agroforestry, deforestation and fertilization (Fig. 3). Results for the remaining land-use classes and their covariables are listed below.

Table 2. Summary statistics for the six highest-ranked meta-analytic models showing degrees of freedom (d.f.), variance explained (R^2), ΔAIC and AIC weights. Model names contain variables and relationships considered: '+' for additive effects, 'by' for interactions

| Model	d.f.	R^2	ΔAIC	AIC weights
Land-use-by-covariable	21	0·281	0·000	0·728
Land-use-by-covariable + plot size	23	0·284	2·592	0·199
Land use + biome	22	0·288	4·633	0·072
Land use + study design	12	0·197	16·875	0·000
Land use + economic region	21	0·265	16·921	0·000
Land use + continent	16	0·221	19·278	0·000
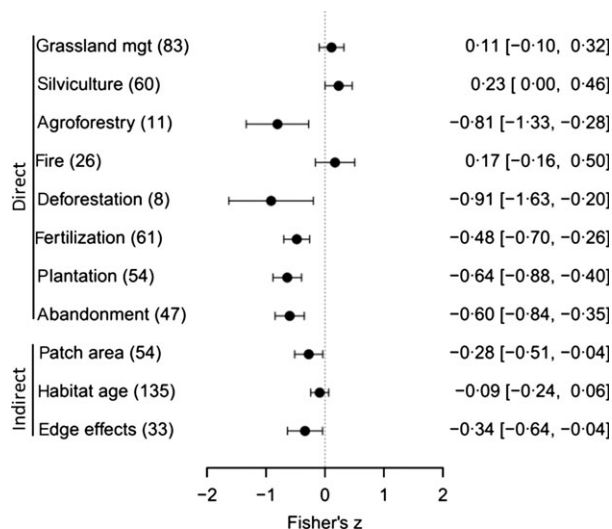
Fig. 3. Effect-size plot from the linear mixed-effects model considering land-use classes as fixed effects. Sequence according to our hypotheses stated in the introduction. Dots and bars represent mean effect sizes and their 95% CI as estimated from the model. Effect sizes indicate the direction and magnitude of the effect of land use on plant species richness. Positive or negative effect sizes suggest whether land use is associated with increases or decreases in species richness, respectively. Number of study outcomes is given in brackets.
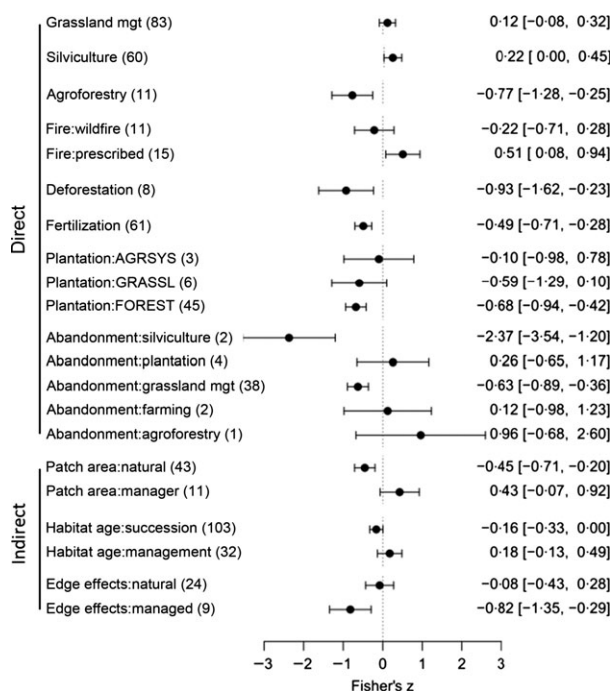
Fig. 4. Effect-size plot from linear mixed-effects models considering land-use-specific covariables, that is, wildfire vs. prescribed fire, initial land-use system for plantations, abandonment of different management classes, patch area of natural vs. managed patches, habitat age of managed vs. abandoned land subject to succession, and edge effects in natural vs. managed patches. Sequence according to our hypotheses stated in the introduction. Dots and bars represent mean effect sizes and their 95% CI as estimated from the models. Number of considered study outcomes is given in brackets. For interpretation of effect sizes, see Statistical methods section and Fig. 3.
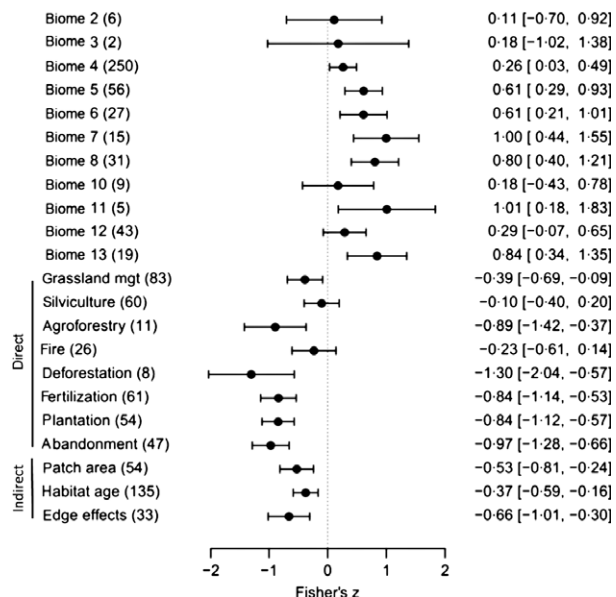
Fig. 5. Effect-size plot from the linear mixed-effects model considering additive effects of land use and biomes. Dots and bars represent mean effect sizes (Fisher's z) and their 95% CI as estimated from the model. Number of study outcomes is given in brackets. For interpretation of effect sizes, see Fig. 3.

GRASSLAND MANAGEMENT

Although we found evidence that grassland management showed a trend towards positive effects, this effect was not significant. Hence, we could not confirm the hypothesis of an overall positive effect.

FIRE

Our results confirmed that fire is mostly positively associated with species richness. Particularly, prescribed fire showed significant positive effects, while evidence was mixed for effects of wildfire.

PLANTATION

Effects of plantations were overall significant and negative. Yet, significant negative effects of plantations on plant species richness mainly became apparent when plantations replaced forest or grassland, rather than agroecosystems.

ABANDONMENT

Abandonment showed significant negative effects and hence led to decreased species richness. In contrast to our expectations, abandonment did not show the inverse effect of the abandoned management itself (cf. Fig. 3): while the abandonment of silviculture and grassland management consistently showed negative effects, abandonment of plantations, farmlands or agroforestry systems was not strongly associated with higher species richness.

PATCH AREA

Land-use expansion, that is, the increase in managed area at the expense of decreasing area of remaining natural land, showed clear negative effects. This result was mainly supported by the large number ($n = 43$) of studies reporting negative associations with species richness when decreasing area of (semi-)natural land. In comparison, the smaller number of studies considering increasing area of managed land ($n = 11$) showed a trend towards positive effects.

HABITAT AGE

Our results were inconclusive for habitat age. Within subgroups, we found our initial hypotheses confirmed: while duration of management was not strongly associated with species richness, temporal proximity to the last disturbance event showed a clear negative effect. In other words, successional age was positively associated with species richness.

EDGE EFFECTS

Our results confirmed that with increasing land-use intensity, species richness is declining in managed patches. In contrast, no clear pattern was found in natural patches, where the intensity gradient goes from the centre towards the edge.

Effects of spatial scale

Our results could not confirm that land-use effects systematically vary with spatial scale. Although the model considering land-use-specific covariables and additive effects with plot size is ranked as the second best model, it is less parsimonious than the model considering land-use-specific covariables only (Table 2). Also, differences between the effects of plot size level in this model were not significant (Fig. S1 in Appendix S4, Supporting information). Furthermore, we found neither general significant additive effects of plot size in the land-use-only model nor evidence for land-use-specific effects of plot size (cf. model considering interactions between land use and plot size).

Effects of biomes

The model ranking (Table 2) suggests that biomes explain most of the effect-size variation across the range of land-use classes. This result indicates that effect sizes are generally dependent on species pool size determined by energy availability and evolutionary history. Specifically, using estimated number of plant species per 10,000 km² as a proxy of species pool size within biomes (Gerstner *et al.* 2014), we found that species pool size is negatively correlated with mean land-use effects per biome (Fig. 6, $r = -0.771$, $P < 0.005$).
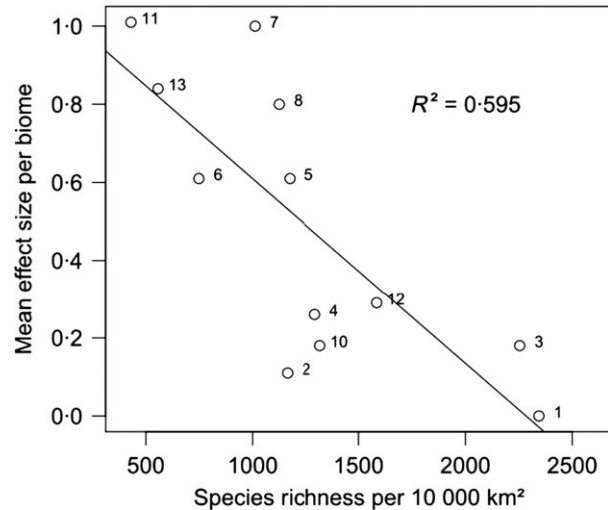
Fig. 6. Relationship between species pool size (i.e. estimated species richness per 10,000 km² *sensu* Gerstner *et al.* 2014) and mean effect size per biome. Numbers refer to biome numbers in Fig. 5 and Fig. S1 in Appendix S3 (Supporting information). Species pool size is negatively correlated with mean land-use effects per biome ($r = -0.771$, $P < 0.005$).

Publication bias

Using Egger's regression, we found no evidence for publication bias, neither in the land-use-only model (intercept $= 0.238$, $P = 0.223$) nor in the land-use-by-covariables model (intercept $= 0.250$, $P = 0.206$), or land use + biome model (intercept $= 0.160$, $P = 0.432$; Appendix S5, Supporting information).

Discussion

LAND-USE EFFECTS ON PLANT DIVERSITY

Our analysis unequivocally demonstrates that land use matters for plant diversity, but that its effects on plant diversity substantially vary (Fig. 3). We detected mostly negative associations between land-use intensity and plant species richness but also positive effects of particular land-use classes such as silviculture and prescribed fire (Figs 3 and 4). These positive associations can be attributed to mechanisms that directly support species coexistence and persistence (e.g. increasing light availability, harvest of dominant species). Most of our hypotheses regarding the direction of land-use effects were confirmed. We only found a few contrasting results:

1. Although agroforestry is a rather extensive land use, our study shows that it consistently lowers plant species richness. This is because agroforestry is mainly applied in tropical regions with high natural plant species richness. Despite its negative effects, agroforestry is considered as extremely important for biodiversity conservation in the fragmented landscapes of the tropics as it establishes passageways between pristine habitats (e.g. Perfecto & Vandermeer 2008).

2. We found no significant effect of grassland management, but a strong trend towards positive associations (Fig. 3). Possibly, this is due to a nonlinear relationship between grassland management intensity and plant species richness (Grime 1973), but also because grazing effects covary with the amount of available nutrients (Proulx & Mazumder 1998): on nutrient-poor sites, species richness declines with increasing grazing pressure, while it increases on nutrient-rich sites.

3. Results indicate a hysteresis of the effects of land-use abandonment: while the abandonment of silviculture and grassland management consistently showed negative effects, the abandonment of plantations, farmlands and agroforestry systems did not show inverse effects of the abandoned management itself, that is, abandonment was not strongly associated with higher species richness. In fact, there are ecological reasons for negative effects of agricultural abandonment especially in landscapes with a long history of cultivation (cf. Rey Benayas *et al.* 2007), but using the very low number of studies (Fig. 4), we were not able to confirm these.

LAND-USE EFFECTS AND SPATIAL SCALE

Effect sizes of ecological drivers (such as land use) on biodiversity might depend on spatial scale due to varying forms of species accumulation curves (SACs) (Chase & Knight 2013). The shape of the SAC is determined by the size of the species pool, the density of individuals, the species abundance distribution and the spatial distribution of species, each potentially affected by land use.

In this study, we included plot size (i.e. spatial grain) as a measure of spatial scale. Because plot size covered a huge range from 0·1 m² to 1000 km², that is, eleven orders of magnitude, spatial scale potentially contributes to the large amount of heterogeneity between study outcomes. However, we could not confirm that land-use effects on plant species richness systematically vary with spatial scale. To further test the robustness of these results, our data set could be complemented by more studies and study outcomes corresponding to other available plot sizes. For example, it is possible that non-significant differences in land-use-specific covariables can collectively create (or eliminate) a statistical difference between plot sizes. This is of special concern when groups have very few studies (e.g. abandonment of farmland or agroforestry).

LAND-USE EFFECTS AND SPECIES POOL SIZE

We would also expect the size of the species pool to influence effect sizes at a given spatial grain and extent, regardless of the true magnitude of the effects (Chase & Knight 2013). For example, differences in effect sizes among communities of varying regional species pool size may be confounded by e.g. comparisons among biogeographic regions (e.g. temperate vs. tropics). The interaction of species pool size with land use is not obvious, however. On the one

hand, effect sizes can potentially be larger in communities with larger local species pool due to the fact that more species can get lost and variation between plots increases. On the other hand, in communities with larger regional species pools, effects may be lower because species can substitute each other locally.

Our results confirm that effect sizes depend on biomes (Table 2, Fig. 5). Specifically, we found a strong negative relationship between species pool size and mean effect size per biome (Fig. 6), suggesting that land use leads to an exchange of species from the same regional species pool. However, species pool estimates based on biomes are highly uncertain and potentially overestimate regional species pools (Lessard *et al.* 2012). Thus, results need further confirmation.

CONFOUNDING EFFECTS AND LIMITATIONS OF THE META-ANALYSIS

In our analysis, we considered the most widespread forms of land use and readily admit that abandonment is actually the absence of land use (but a direct result of land-use decisions and hence in our view qualifies as land use itself). For achieving a representative rather than a complete sample of studies, we excluded the small number of studies we found on several other land-use types, such as restoration through afforestation, herbicides/pesticides and browsing. We might have missed some less common land-use types and therefore plea for the development of an overarching and consistent land-use classification scheme that enables scientists and practitioners to appropriately characterize local land use and at the same time be able to make regional and global comparisons of drivers and environmental effects.

In total, we found 1911 studies in our literature search but only considered about one-sixth ($n = 375$) in our meta-analysis. This was mainly due to strict inclusion criteria regarding form and content, but a considerable part of studies had to be excluded due to insufficient reporting and statistical issues (Hillebrand & Gurevitch 2013). For a case study to be useful in meta-analyses, data requirements are quite stringent. Without reporting meaningful statistics, case studies cannot be used for quantitative synthesis. Therefore, we recommend that case study authors as well as reviewers and editors ensure that the statistics are reported with sufficient detail for further analysis (e.g. provide data also for non-significant results, not only *P*-values).

Our data set is regionally biased with Europe and North America being overrepresented and the majority of countries (73·5%) not represented in the data base (Fig. 2). Geographical bias of applied ecological studies has been reported repeatedly (Keddy 1989; Martin, Blossey & Ellis 2012). This might be caused by restrictive search criteria, such as the restriction to published journal articles written in English, but could also reflect regional differences in the perception of land-use issues. For example, fertilization was found to be an important issue only

in the northern hemisphere, while from the southern hemisphere, not a single study on fertilization effects was included. In concordance, global fertilization maps show the uneven distribution of fertilizer inputs in the northern hemisphere (Potter *et al.* 2010). Abandonment of land use is mainly an issue in Europe, where increasing global markets and urbanization among others lead to rural abandonment (Lambin *et al.* 2001; Navarro & Pereira 2012). Finally, agroforestry is common in the tropics, but not in temperate regions.

A common criticism on meta-analyses is the comparability between studies. To account for differences, we examined several covariables. Still, we might have missed some potentially important variables. First, studies often consider different temporal scales when they either compare sites with different land uses (i.e. space-for-time substitution) or compare sites before and after land has been used (i.e. before–after comparisons). By matching both groups, we assume that space-for-time studies are minimally affected by differences between sites, for example due to environmental heterogeneity, and that before–after comparisons used an appropriate time-scale to detect diversity changes. Furthermore, studies often report effects only for specific plant species subgroups, for example woody, non-woody, native or exotic. Unfortunately, classification of subgroups greatly differed and hence impeded more detailed analyses. We tried to be as comprehensive as possible and used statistics for the most integrative group of plants in each study.

The effects of land use on plant diversity are further determined by the diversity measure (Gibson *et al.* 2011; Chase & Knight 2013). We only considered species richness as a response variable since this is the most widely used measure of ecosystem performance and commonly hypothesized to support ecosystem functioning (Hooper *et al.* 2005; Isbell *et al.* 2011). However, when land use is accompanied with profound ecosystem transformation (e.g. deforestation), species richness changes might be irrelevant for understanding changes in ecosystem functioning (Vellend *et al.* 2013) and a focus on other measures of species diversity and composition may reveal further insight. For example, species restricted in their range or specialized to a certain habitat are especially threatened by habitat transformation while other species might benefit. Thus, although local species richness might not be affected, a considerable amount of species may be lost while others are introduced. Ultimately, this form of species replacement is of concern because it results in a reduction in genetic diversity and homogenization of floras (Sax & Gaines 2003).

CONCLUSIONS

A consistent characterization and mechanistic understanding of land use, land management and land-use intensity is highly important for a global assessment of the decline of plant species richness. This extensive synthesis provides, to our knowledge, the most comprehensive and quantitative overview to date about effects of the most widespread and relevant land-use options on plant diversity. We found strong patterns in the data confirming ecological theory but little support that land-use effects can be generally explained by their environmental and socioeconomic context. We found a number of caveats and open questions and thereby provide a new vantage point for researchers and define the most topical and important questions to which we need answers. We expect that analyses of other taxa, which are currently lacking, may reveal similar patterns, identifying important variables, explaining increases or decreases in species richness and thus providing better insights into the relationships between land use and ecosystems.

Data accessibility

All data are presented in the supporting information.

Author contributions

KG collected data. KG, CFD, AS and AMM performed the meta-analysis. KG wrote the first draft of the manuscript. All authors contributed substantially to revisions.

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Supporting Information

Additional Supporting Information may be found in the online version of this article.

Appendix S1. Search terms and table of meta-analyses considered for the search of case studies, their characteristics and references.

Appendix S2. Table of effect sizes and corresponding study characteristics and studies used in the meta-analysis.

Appendix S3. Detailed methods on data extraction and covariables coded.

Appendix S4. Summary statistics for all meta-analytic models and effect size plots for the land use-specific covariables and additive effects with plot size level.

Appendix S5. Publication Bias: Funnel plot of effect size standard error plotted against model residuals.