Conventional land-use intensification reduces species richness and increases production: A global meta-analysis

Running head: Land-use, species richness and production

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Abstract

Most current research on conventional land-use intensification addresses its potential to either threaten biodiversity or to boost agricultural production. However, little is known about the *simultaneous* effects of conventional intensification on biodiversity and yield. To determine the responses of species richness and yield to conventional intensification, we conducted a global meta-analysis synthesizing 115 studies which collected data for both variables at the same locations. We extracted 449 cases that cover a variety of areas used for agricultural (crops, fodder) and silvicultural (wood) production. We found that, across all production systems and species groups, conventional intensification is successful in increasing yield (grand mean +20.3%), but it also results in a loss of species richness (-8.9%). However, analysis of sub-groups revealed inconsistent results. For example, small intensification steps within low intensity systems did not affect yield or species richness. Within high-intensity systems species losses were non-significant but yields gains were substantial (+15.2%). Conventional intensification within medium intensity systems revealed the highest yield increase (+84.9%) and showed the largest loss in species richness (-22.9%). Production systems differed in their magnitude of richness response, with insignificant changes in silvicultural systems and substantial losses in crop systems (-21.2%). In addition, this meta-analysis identifies a lack of studies that collect robust biodiversity (i.e. beyond species richness) and yield data at the same sites and that provide quantitative information on land-use intensity. Our findings suggest that, in many cases, conventional land-use intensification drives a trade-off between species richness and production. However, species richness losses were often not significantly different from zero, suggesting even conventional intensification can result in yield increases without coming at the expense of biodiversity loss. These results should guide future research to close existing research gaps and to understand the circumstances required to achieve such win-win or win-no-harm situations in conventional agriculture.

Introduction

While some human-managed lands can provide benefits for the protection of individual species (e.g. Loos et al., 2014), the need to use land for the production of food and other goods is generally at odds with biodiversity conservation (Green et al., 2005; Foley et al., 2011; McShane et al., 2009; Cardinale et al., 2012). Today, the majority of Earth's land surface has been transformed by human activities and is subject to some kind of human land use, like agriculture, settlement, infrastructure or mineral extraction (Hooke & Martín-Duque, 2012). There is indication that land conversion has slowed down while the production of food and natural materials still continues to increase (Seppelt et al. 2016). This raises concerns that – besides land conversion – land-use intensification poses a major threat to biodiversity (Perreira et al., 2010; Maxwell et al., 2016), as changes in land-use intensification typically result in a loss of species (Gerstner et al., 2014; Kehoe et al., 2015; Newbold et al., 2015).

The importance of land use for biodiversity and the provision of goods has been widely acknowledged in conceptual (e.g. Clough et al., 2011; Tscharnke et al., 2012; Seppelt et al., 2017; Fischer et al. 2017a) and empirical studies (e.g. Gerstner et al., 2014). However, recent scientific debates on closing yield gaps or conserving biodiversity in agroecosystems have addressed the effects of land use either on agricultural production *or* biodiversity conservation (e.g. Newbold et al., 2015; Mauser et al. 2015; but see Denmead et al., 2017, Garibaldi et al., 2017; Egli et al., 2018). A notable exception that includes both perspectives is the land sharing-sparing framework (Chappell & LaValle 2011; Phalan et al., 2011a; 2011b). Although being criticized for lacking applicability to many real landscapes as it ignores questions of scale (e.g. Fischer et al., 2014; von Wehrden et al. 2014), the sharing-sparing framework has sparked a lively discussion within the scientific community. In order to better understand trade-offs between agricultural production and biodiversity in general, as well as to provide additional insights for on-going debates, a quantitative review or meta-analysis synthesizing the studies that have measured the simultaneous effects of land-use intensification on species richness and yield in the field (e.g. Gabriel et al., 2013; Norvez et al., 2013) is still lacking.

There are multiple different pathways of land-use intensification such as conventional intensification (focusing mainly on increasing inputs to boost outputs), ecological intensification (replacement of inputs by including ecosystem services management; Bommarco et al., 2013; Geertsema et al., 2016) or sustainable intensification (producing more yield with less environmental impact; e.g. Godfray & Garnett et al., 2014). Such different intensification steps may be called “conventional”, “organic” or “nature friendly”, labels that can have different meanings depending on the location (e.g. Seufert et al., 2017). Here we focus on conventional land-use intensification in agricultural and silvicultural production systems. The type and extent of land use vary considerably and are highly dependent on biophysical conditions, national priorities, policies, local needs as well as the availability of technologies and knowledge (van Asselen & Verburg, 2013; Václavík et al., 2013). Conventional land-use intensification can range from slight alterations in management practices to a substantial reshaping of landscapes; it can involve small increases in manual labour but also the use of large machinery, whilst potentially making use of natural products for fertilization and pest control or the broad-scale application of chemicals for the same purposes. In order to compare land-use intensity at a global scale and across different production systems, we here define conventional land-use intensity as changes in management practices (input and harvest intensity) that aim to increase production on already used land (see Box 1 for details).

Studies addressing the effect of conventional intensification on species richness and yield on continental or global scales often incorporate data generated by models or country-scale statistics (e.g. FAO agricultural statistics; Kehoe et al., 2015; Delzeit et al., 2016). While there have been numerous studies collecting field data on both agricultural or silvicultural production and species richness within a defined area, a global analysis synthesizing such data has yet to be conducted. It remains, for example, unclear whether a steady increase in yield and decrease in species richness along a gradient of conventional land-use intensification can be found, whether both species richness and yield can be increased at the same time or whether smaller decreases in species richness for a given increase in yield are possible (Fischer et al., 2014; Seppelt et al., 2016). Understanding changes in species richness within production systems is important aside from conservation concerns. Species support key ecosystem functions and services within agricultural landscapes (e.g. Klein et al. 2003), although the details of these relationships still remain unresolved in many cases (e.g. Isbell et al., 2017; but see Seabloom et al., 2017). A global meta-analysis addressing the simultaneous effects of conventional land-use intensification on species richness and yield can provide new insights into such open questions and complement the recent literature by providing quantitative synthesis. In addition, it can identify important research gaps and, thus, help steer future research towards addressing them.

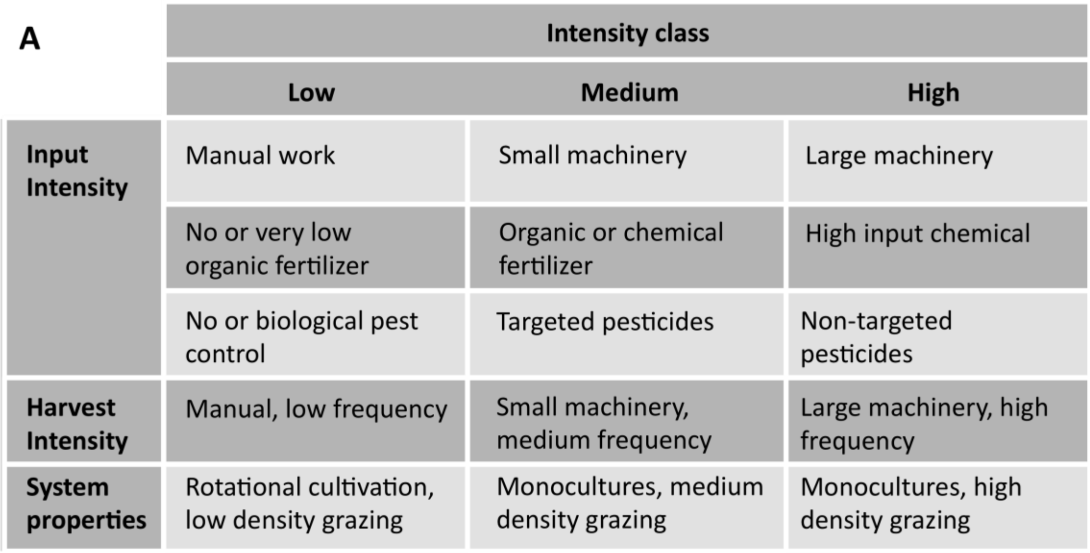
Consequently, we here investigate the relationship between conventional intensification, species richness and yield, by synthesizing the published literature that collected these data in the same locations (i.e. in habitats from which humans extract biomass). In order to fully capture the effects of conventional intensification, this study focuses solely on those habitats used for human land use and does not compare non-used (i.e. natural) to used habitats as done in several previous studies (e.g. Newbold et al., 2015). With this meta-analysis we further try to identify whether a general trade-off between species richness and yield is detectable and if there is evidence for situations in which yield can be increased with simultaneous positive or neutral effects on species richness. To quantitatively compare studies along a gradient of conventional land-use intensification, we developed a general scheme for classifying land-use intensity. We categorized conventional land-use intensification steps that are comparable across different landscapes globally and between different production systems (wood, green fodder, crops), and that take into account the initial land-use intensity and the magnitude of intensification (see Box 1 for details). We focus on production-species richness trade-offs, but exclude other aspects of the multifaceted food-security and sustainability debates (e.g. long-term yield stability, economic profits; Fischer et al., 2017a; Seppelt et al., 2017; Fischer et al., 2017b; German et al., 2017). In order to unpack the various facets of the intensification-species richness-production relationship, we structure this meta-analysis to highlight the following contrasts in examining impacts on each of them:

a) Conventional land-use intensification out of low-intensity systems;

b) Conventional land-use intensification in medium-intensity systems; and
c) Conventional land-use intensification in high-intensity systems.

As the effects of land-use intensification on species richness may depend on taxa, product type, land-use history and climate, we investigated whether the relationship between species richness and yield is influenced by these factors. Specifically, we addressed whether production systems based on slow growing products, such as wood, would show the same magnitude of response in species richness or yield to intensification as those based on fast growing products (i.e. crop and fodder systems; Gerstner et al., 2014; Newbold et al., 2015). In addition, we investigated if mobile species groups such as vertebrates and invertebrates are less affected by land-use intensification than stationary species (i.e. plants; e.g. Clough et al., 2011) within the production system analysed. We further investigated if areas having a longer history of land-use showed smaller responses to land-use intensification than areas with shorter land-use history (Ellis et al., 2013) and whether large-scale climate zones distinctly differ in their responses to intensification (Perring et al., 2016). Furthermore, we checked if the results were robust across different units of yield, harvested crop species, if species richness and yield were measured from the same species group or if data was collected at different plot sizes.

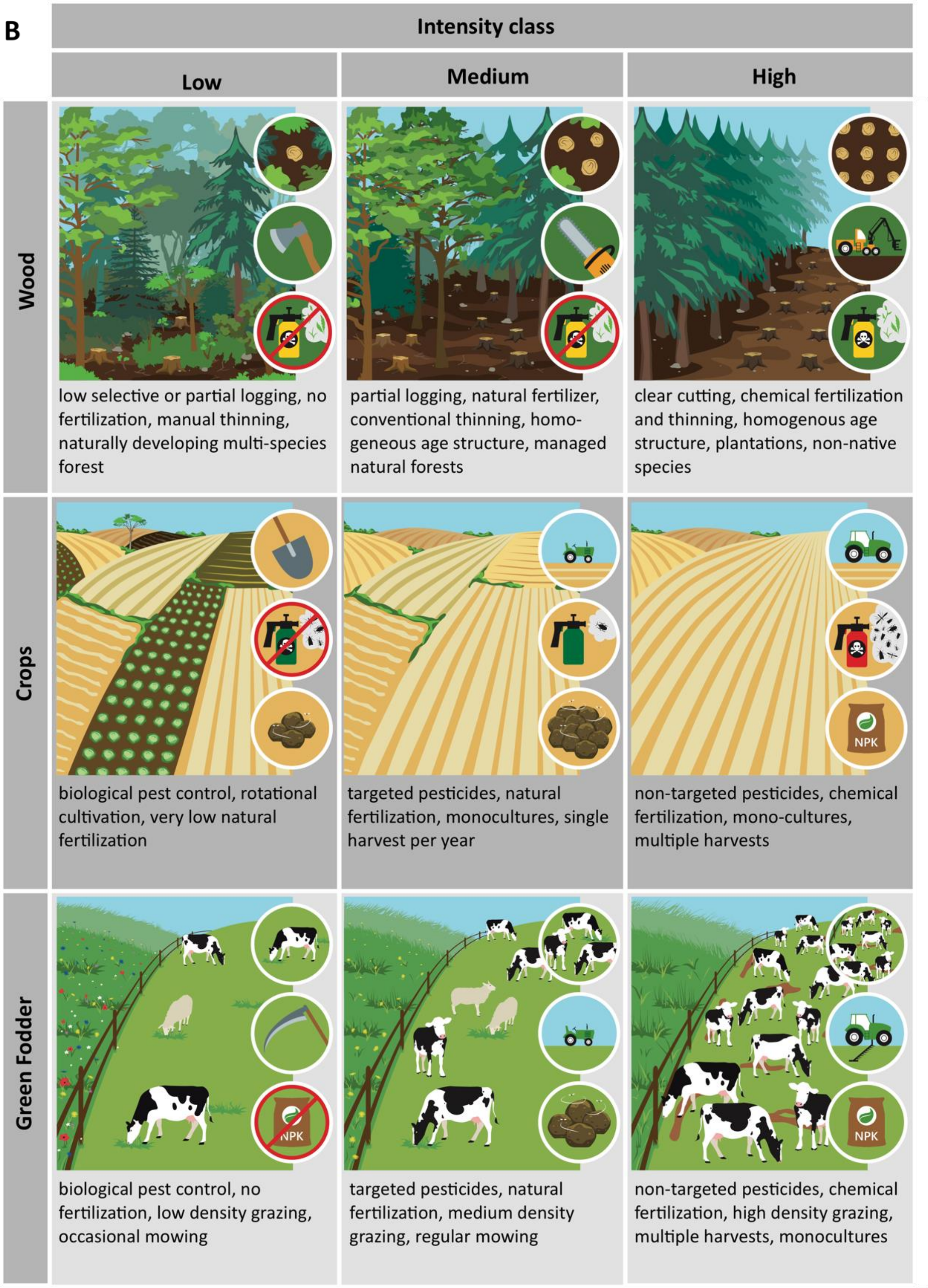
Box 1 | Illustration of the framework used for the identification of land-use intensity classes and intensification steps. We defined conventional land-use intensity as a combination of input intensity (e.g. amount of fertilizer/pesticide application) and harvest intensity (e.g. type of harvest, number of harvests per year) which allows for comparisons across production systems and regions (Hudson et al., 2014), Figure A.

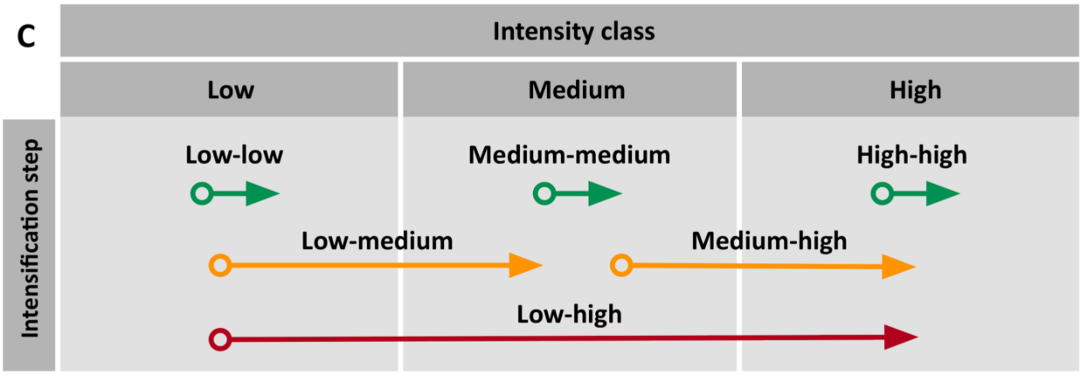


A

	Intensity class		
	Low	Medium	High
Input Intensity	Manual work	Small machinery	Large machinery
	No or very low organic fertilizer	Organic or chemical fertilizer	High input chemical
	No or biological pest control	Targeted pesticides	Non-targeted pesticides
Harvest Intensity	Manual, low frequency	Small machinery, medium frequency	Large machinery, high frequency
System properties	Rotational cultivation, low density grazing	Monocultures, medium density grazing	Monocultures, high density grazing

We defined three broad land-use intensity classes: “low”, “medium” and “high” separately for each of the globally most common production systems: “crops”, “wood” and “green fodder”. Figure B illustrates and lists specific aspects of the land-use intensity for each of these production systems (see also Appendix S3). Conventional land-use intensification steps (“low-low”, “medium-medium” and “high-high”, “low-medium”, “medium-high and “low-high”) were then formed to classify each study case (Figure C, yellow and red arrows, see Methods for detailed description).


B
Intensity class
Low
Medium
High
Wood
low selective or partial logging, no fertilization, manual thinning, naturally developing multi-species forest
partial logging, natural fertilizer, conventional thinning, homogeneous age structure, managed natural forests
clear cutting, chemical fertilization and thinning, homogenous age structure, plantations, non-native species
Crops
biological pest control, rotational cultivation, very low natural fertilization
targeted pesticides, natural fertilization, monocultures, single harvest per year
non-targeted pesticides, chemical fertilization, mono-cultures, multiple harvests
NPK
Green Fodder
biological pest control, no fertilization, low density grazing, occasional mowing
targeted pesticides, natural fertilization, medium density grazing, regular mowing
non-targeted pesticides, chemical fertilization, high density grazing, multiple harvests, monocultures
NPK
NPK



Example 1: Summerville et al. (2002) is a study conducted in a wood-production system (top row in Figure B) that compared species richness of arthropods in selectively logged (coded as intensity class: “low”) and clear-cut forests (intensity class: “high”). In both treatments they also quantified basal area of marketable trees. We used this data to form one “low-high” case (Figure C, red arrow) for the response of arthropod richness to the two logging treatments and one “low-high” case for the response of marketable tree basal area to the same treatment.

Example 2: The study of Batary et al., (2013) took place in a crop production system (middle row in Figure B), where the authors compared low input organic farming (coded as “medium intensity” on the conventional intensification gradient) with high input conventional farming (“high intensity”). The study reports tons of wheat harvested per hectare as a measure of yield and species richness for plant species, arthropods and birds. We used this data to form four “medium-high” cases (Figure B, yellow arrow), three cases for the response of richness to the two levels of intensification (one for each species group) and one case for the production of wheat.

Example 3: Mudrak et al. (2013) investigated biomass production and plant species richness in a green fodder system (bottom row in Figure B). The study compared three treatments: mulching once annually with high stubble (which we coded as “low intensity”), mowing once annually with high stubble (also coded also as “low intensity” but with increased levels) and mowing twice annually with low stubble (coded as “high intensity”). Two of the treatments fall within the “low intensity” class but can be distinctly separated into a baseline and an increased treatment, allowing us to compare the treatments within the “low intensity” class. We used this data to form two cases each for biodiversity and yield, based on the “low-low” (Figure C, green arrows) and the “low-high” comparison (red arrow). Similarly, studies that investigated the effects of high intensity agriculture reducing or omitting individual aspects thereof (e.g. fertilized and pesticide treated coffee plantations with and without irrigation, Boreux et al., 2013) were used to form “high-high” comparison cases in this meta-analysis.

Material and Methods

Literature search and screening protocol

We conducted a systematic review in compliance with the Preferred Reporting Items for Systematic Reviews and Meta-Analyses (PRISMA) framework (Moher 2009; see Appendix S1). We searched the Web of Science database for search terms related to land use, biodiversity and yield (see Appendix S2 for the full search term and all refinement options employed). We included all articles published since January 1st 1990 in English or Spanish. The final search resulted in 9,909 studies.

We included studies meeting the following selection criteria: Studies had to measure both species richness and yield in the same site in response to the application of land-use conventional intensification. In this way, we included studies that measured the effect of conventional intensification on several sites in response to different intensities (i.e. space-for-time substitutes). Out of the full initial set of papers, we manually screened the abstracts of 6,116 studies and retained studies only if they contained information about land use, species richness, and/or yield. In order to filter the remaining 3,793 studies, we used a machine-learning algorithm based on ensembles of Support Vector Machines (SVMs) developed for systematic reviews of the medical literature (Wallace et al., 2010). The machine-learning algorithm correctly identified 84% of the manually screened studies as being relevant, with a specificity of 51% (standard deviation 0.016), i.e. the model eliminated half of the irrelevant. The full text documents of all studies identified as potentially relevant

(1371), both screened manually or through machine learning, were acquired and processed further, see Appendix S1 and S5.

Data extraction and validation

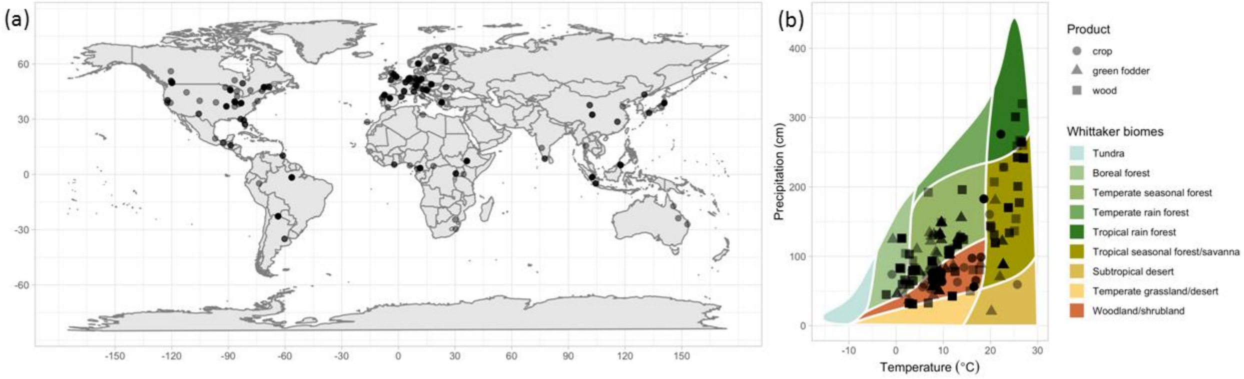


Figure 1 | Locations of sites included in the meta-analysis. **(a)** Sites of the 449 cases (292 for species richness and 157 for yield) that were extracted from 115 studies (see S13 for a complete list of references). At each site data on species richness and yield in response to conventional land-use intensification was collected. **(b)** Illustrates the distribution of sites and cases across climate zones in a Whitacker plot. If several cases were located at the same sites, the points are overlaid and thus darker.

From the initial 1,371 studies, 115 studies had sufficient data to be included (see Figure 1 for a global distribution of the studies). Means, standard deviations and sample sizes for control (lower land-use intensity) and treatment (higher land-use intensity) were extracted from the text, tables or figures (using ImageJ; Schneider et al., 2012). If data were not completely available in the main document and the supplementary material, we requested them from the corresponding author. Studies that did not report means or sample sizes were excluded from the analysis. This resulted in a total of 115 studies that were used in subsequent analyses (see Appendix S12 for the full list of references). Data coding and data review were undertaken by eight of the co-authors. Initially, studies were coded as a group to assure inter-coder consistency and reliability. Subsequently, frequent internal reviews were conducted to maintain consistency. Each document was coded by at least two of the co-authors. Each of the studies we incorporated in this meta-analysis had to include, both, information on species richness and yield in response to conventional land-use intensification in the same locations. The measurements for both variables also had to be collected at the same area (but possibly in differently sized plots), excluding studies that, for example, measured species richness in plots or landscapes and used coarser-scale statistics (e.g. sub-national) for yield. We assume that the original study authors sampled yield and species richness using appropriate spatial units for both. Based on the type of product that was harvested we first classified the production system (crop, green fodder or wood) according to the description of the land use provided in the original paper.

Land-use intensity and intensification classification

We used a classification system for land-use intensity based on a pre-defined set of management practices. We defined land-use intensity based on energy use and labour as a combination of input intensity (e.g. type of fertilizer/pesticide application) and aspects related to output or harvest intensity (e.g. type of harvest, number of harvests per year) but not the actual outputs (i.e. yields) themselves in order to avoid circularity. While this conceptualization of intensification will identify more intensive systems based on the type of management practices implemented (e.g. no fertilizer vs. organic vs. chemical fertilizer), it does not classify land-use intensity based on quantities of a management practice (e.g. kg nitrogen applied per area). Thus, our classification of intensification best reflects conventional intensification, rather than other forms of intensification (e.g. sustainable intensification in agriculture;

Rockström et al., 2017) and it also allows for comparisons across production systems and regions (Hudson et al., 2014; Box 1).

For studying a gradient of land-use intensification steps we first defined three broad land-use intensity classes: “low”, “medium” and “high”, with separate criteria for each of the globally most common production systems: “crops”, “wood” and “green fodder”. Figure B in Box 1 illustrates and lists specific aspects of the land-use intensity for each of these production systems (see also Appendix S3). In a second step, we distinguished different degrees of conventional land-use intensification within each study in order to form intensification cases for the subsequent analysis. Land-use intensification could occur in small steps, meaning an increase of pre-existing management activities that does not lead to substantial changes in the production system (i.e. no change of land-use intensity class). In this way, cases for the intensification steps “low-low”, “medium-medium” and “high-high” were formed (Figure C in Box 1, green arrows). More substantial changes in land-use may lead to a change of a production system into another land-use intensity class, resulting in cases covering the “low-medium”, “medium-high and “low-high” intensification steps (Figure C in Box 1, yellow and red arrows).

By including measurements for different species groups and/or types of yield, a publication could provide several cases of land-use intensification (e.g. one response of crop yield and the responses of plants, birds and insects to a given intensification step would result in three species richness cases and one yield case) leading to unequal numbers of cases for species richness and yield.

Case extraction from all 115 studies and based on different land-use intensification steps, taxa, or product types as described above, resulted in a total of 449 cases, 292 cases for species richness and 157 for yield (see Appendix S13 for full tables of coded data including raw species richness and yield data).

Species richness, abundance and yield measure extraction

Biodiversity was quantified using species richness (i.e. numbers of species), as reported by the original study authors. When species abundances were provided, species richness was calculated as the total number of species with at least one recorded individual. In 19 out of the 115 studies the original study authors provided measures of Shannon diversity (11 studies) or published abundance information that allowed us to compute Shannon diversity (8 studies) in addition to species richness data. All subsequent analyses performed with this subset of studies for which we could extract or calculate Shannon diversity and the results are described in Appendix S12. Species were grouped into three groups of taxa: vertebrates, invertebrates, and plants. If the method for measuring species richness was area-based (in contrast to transect walks or sweeps), we extracted the plot size or area used to measure species richness and converted to square metres if necessary.

Yield was most commonly reported as a mass-per-area (e.g. tons per hectare), or volume-per-area (e.g. cubic meter of timber per hectare). All products were assigned to one of the three product-types: crops, green fodder, and wood. We always coded the provided measure of yield that was as close as possible to the final product (i.e. if a study on cacao plantations reported annual cacao harvest and wood volume of the cacao trees, we included only the cacao yield). Multiple crops on the same area or multiple harvests per year were treated individually and coded as separate cases.

For approximately two thirds of the forest studies yield was not reported in mass per area or volume per area units. Here, we used the nearest available information given by the authors of the study on standing biomass of commercially relevant trees such as basal area or total volume of standing biomass (area-per-area measurements). Although these measures are proxies, they have previously shown to be reliable predictors for harvest yields of many commercial tree species: for example, although more complex models are suggested, Júnior et al. (2014) show that basal area already explains 97% of the variability in estimating above ground biomass. Especially as we here focus on relative yield change, we expect any deviations due to nonlinearities to be small. Nevertheless, we tested for any dependence of average yield changes on the unit of measure used (Appendix S9). Additionally, in forest systems the final harvested amount of wood was only rarely available directly in the studies. According to the information provided by the authors we carefully interpreted the given change in yield. Internal reviewing of these critical cases was used to verify the interpretation of results.

In order to test whether effects of land-use intensification varied according to the environmental context, we assigned each study location to one of five climate zones according to the Köppen-Geiger classification (Kottek et al., 2006): tropical climate; arid climate; temperate climate; cold, continental climate; polar climate (see Appendix S4 for details).

To analyse each study location according to their land-use history (i.e. length of human land use at this location) we developed a classification to represent five main land-use history classes characterized by major developments in agriculture and silviculture (Vasey, 2002; Mazoyer & Roudart, 2006): Origin of agriculture; Expansion of agriculture; Middle Ages; Modern agriculture and Green Revolution (see Appendix S6 for details). We applied these classes to a global dataset dating back to 5950 B.C. (KK10 dataset; Ellis et al., 2013) which describes the proportion of land within 0.1°× 0.1° grid cells that has been used by humans in time steps of 50 years.

For each study case, we extracted the date of first significant use (defined as 20% of human-used area within a grid cell). Although the history of land use for the specific plots sampled is likely to explain better the observed differences in yield and species richness than are the coarse-scale estimates used here, such information is almost never available. Nevertheless, previous studies have shown that coarse, landscape-scale land-use history is useful for explaining biodiversity responses to land use (Newbold et al., 2015).

Data analysis and statistical methods

Using the extracted means, standard deviations and sample sizes for both lower-intensity control and higher-intensity treatment, we calculated log-transformed response ratios and variances (Koricheva et al., 2013). The response ratio can be interpreted as the species richness or yield of the higher-intensity land-use as a proportion of that in the lower-intensity. Hence, a response ratio of 1.0 signifies no change; and, for example, a value of 0.8 indicates 80% of the species or yield remains after intensification (i.e. 20% loss). Log-transformed response ratios were used in the analyses but were back-transformed and converted to percentage change for ease of interpretation in the results presented.

We imputed missing data for standard deviations (169 out of 449 cases) based on predictive mean matching using the R package mice (version 2.22; van Buuren & Groothuis-Oudshoorn, 2011). The relationship between observed means of response ratios, standard deviations and number of samples was first fitted to the subset of data without missing values. Multiple imputation chains were then generated using Gibbs sampling, i.e. a random draw from the posterior predictive distribution of model coefficients. We imputed missing standard deviation values using the mean of 50 imputation chains.

We analysed variation in species richness and yield effect sizes using linear mixed-effects meta-analysis models (in R version 3.0.1 using the function rma.mv, in the package metafor version 1.9.8; Viechtbauer, 2010). This function is particularly designed for performing multilevel meta-analyses. We used restricted maximum likelihood to estimate mean effect sizes and their variances, and maximum likelihood estimation to compare the goodness-of-fit between models. The models tested are specified in the caption of Table 1.

We accounted for (1) non-independence of observations from the same study, and (2) non-independence from relatedness of multiple intensification steps within one study by specifying covariances between effect sizes X and Y as,

$$cov(X,Y) = cor(X,Y) * sqrt(Var(X)) * sqrt(Var(Y)),$$

where $cov(X,Y)$ is set to 0.5 if X and Y belong to the same study and share a control or treatment, because effect size X determines 50% of effect size Y and vice versa. All models were fitted using case nested within study as random effects to account for dependencies of multiple outcomes within the same study (Nakagawa & Santos, 2012). The covariates “land-use intensity step”, “species group”, “product”, “main climate zone” and “land-use history” were fitted as fixed effects.

We compared three models for species richness and three models for yield, using different sets of covariates (Table 1): (i) a model containing “land-use intensification step” as a single explanatory factor; (ii) a model that additionally contained “species group” and “product” (for yield the model contained “product” only) and their interactions with “land-use intensification step”; and (iii) a model that additionally include “land-use history” and “climate” and their interaction with “land-use intensification step”. We evaluated the goodness-of-fit of the models using various statistics provided by the R-package metafor since there is no consensus on a single best fit statistic: *AICc*, and *BIC* as measures of overall model fit, the model heterogeneity Q_M (Hedges & Olkin, 1984) and its *p*-value of statistical significance, the unexplained (or sampling) heterogeneity Q_E, and the proportion of observed variance explained by the model, calculated as the ratio of Q_M to $Q_T = Q_M + Q_E$. The ratio is comparable to the R^2 value from linear regressions but uses the ratio of weighted sums of squares. Finally, we provide I^2 as a measure of the amount of heterogeneity within studies (I^2(Study ID)) and within study cases (I^2(Study Case)) relative to the total heterogeneity (Nakagawa & Santos, 2012). For the models of yield, species group is not considered a relevant explanatory variable and is therefore not included. We validated the suitability of our land-use intensification classification by performing a likelihood ratio test comparing the intercept-only model and the model containing only land-use intensity. For both richness and yield models the tests were significant ($p<0.0001$), thereby confirming larger between-group than within-group variation.

We compared mean percentage change of species richness and yield predicted by the models. Mean effects of land-use intensification were considered significant if their 95% confidence intervals (CIs) did not cross zero. To test pairwise differences of factor-level effects for land-use history and climate, we averaged model predictions of the full model (containing all covariates) across land-use intensification steps, species groups, and products and performed pairwise *t*-tests with the Holm-correction for multiple comparisons (Appendix S7). If distributions of effect sizes within groups are normal, both tests (pairwise *t*-test and boxplot) result in the same conclusions (Crawley, 2012). If distributions are skewed, however, conclusions may differ.

We explored possible correlated or confounded variables in our dataset, including 1) measuring species richness and yield on the same organism group (for example, in grassland systems where species richness and yield may both be derived from the same plants); 2) direct linkage of yield to land-use intensity (e.g. through harvesting techniques such as clear-cuts or selective logging); 3) measures of yield expressed in very different terms; or 4) the dependence of species richness on spatial scale.

All code, performing the analysis as described in the Methods is available at GitHub: https://github.com/KatharinaGerstner/LUBDES_MA and all underlying data is available in Appendix S13.

Results

When considering all possible intensification steps, product types and species groups together, we found that conventional land-use intensification leads to a significant overall gain in yield (+20.3% [95% confidence interval: +8.9, +33.0], number of cases n=157), and significant loss of species richness (-8.9% [-14.0, -3.5], number of cases n=292; grand mean in Figure 2). None of the conventional intensification steps provide a statistically significant indication that yields and species richness could be increased at the same time (Figure 2). Situations, in which conventional intensification increases yield but with no significant effect (although with negative mean values) on species richness, were identified: intensification within the high-intensity land-use class (Figure 2; species richness: -6.1% [-12.5, +0.8], n=65; yield: +15.2% [+3.1, +28.7], n=39), medium to high intensification (species richness: -6.3 [-12.3, +0.2], n=81; yield: +24.3% [+11.6, +38.5], n=39) and low to high (species richness: -12.1% [-25.2, +3.4], n=31; yield: +28.8% [+7.5, +54.3], n=14). It is important to note that these results exhibit strong heterogeneity among studies (Table 1a, b), with a range of impacts in individual studies on both species richness and yield within individual land use intensification classes.

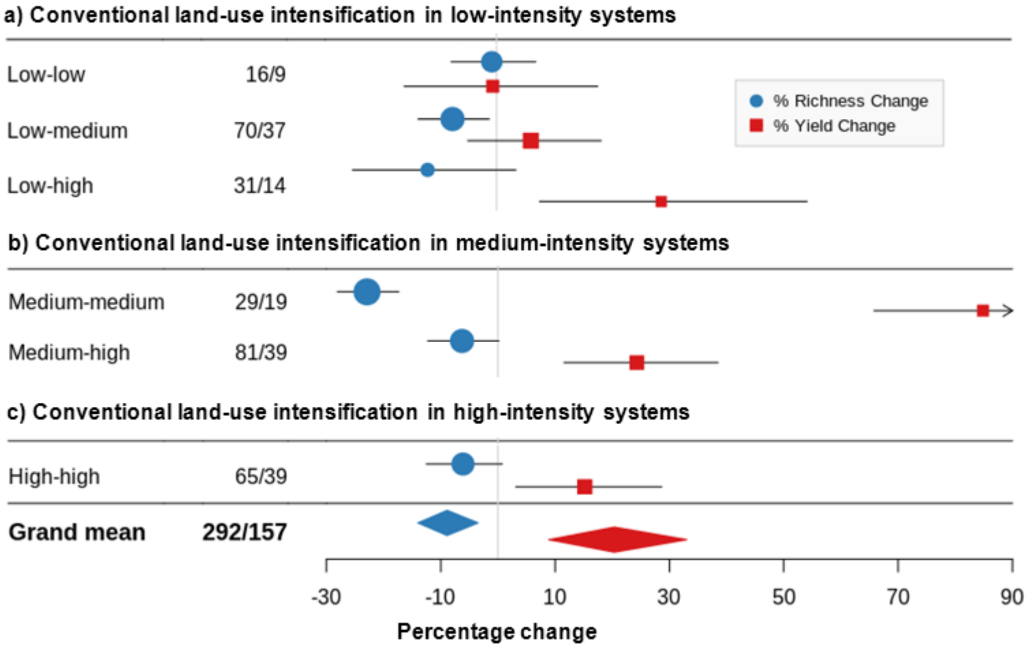


Figure 2 | Change in species richness and yield as a result of conventional land-use intensification. Mean percentage change in species richness and yield to conventional intensification steps (1st column). The number of samples for species richness/yield cases is given in the 2nd column. Numbers of studies from which these cases were extracted are given in Appendix S8. Error bars and horizontal points of the diamonds show 95% confidence intervals. The arrow denotes a confidence interval larger than axes. Effect sizes were calculated and analysed using log response-ratios, which were back-transformed and converted to percentage change. Results shown are based on 449 cases and are derived from the full models as shown in Table 1a and 1b.

Table 1 | Goodness-of-fit statistics for meta-analysis models. (**a**) species richness, (**b**) Yield. Abbreviations: *ΔAICc* = Akaikes' Information Criterion and *ΔBIC* = Bayesian Information Criterion expressed as the difference of each model compared with the best-fitting model; Q_M = model heterogeneity; Q_E = unexplained (or sampling) heterogeneity; p(Q_M) = proportion of observed variance explained by the model calculated as the ratio of Q_M to $Q_T = Q_M + Q_E$. See Appendix S4 for more details.

a) Species richness (n = 292 cases)

	ΔAICc	*ΔBIC*	Q_M	p(Q_M)	Q_E	R^2	I^2 (Study	I^2 (Study

							ID)	Case)
Intercept only	639.727	445.047	9.972	0.002	9321.492	0.001	0.806	0.194
Land-use intensification step	425.804	249.082	233.614	<0.001	9204.254	0.025	0.764	0.236
Land-use intensification step + species group + product type	86.784	0.000	636.242	<0.001	7022.391	0.083	0.666	0.334
Land-use intensification step + species group + product type + climate + land-use history	0.000	13.217	830.355	<0.001	5674.327	0.128	0.750	0.250

b) Yield (n = 157 cases)

	ΔAICc	*ΔBIC*	Q_M	p(Q_M)	Q_E	R^2	I^2 *(Study ID)*	I^2 *(Study Case)*
Intercept only	3670.744	3572.330	13.132	<0.001	10794.128	0.001	1.000	1.5E-07
Land-use intensification step	899.511	815.562	2794.798	<0.001	8899.404	0.239	1.000	2.5E-07
Land-use intensification step + product type	562.226	509.749	3161.938	<0.001	6646.924	0.322	0.475	5.3E-01
Land-use intensification step + product type + climate + land-use history	0.000	0.000	3863.682	<0.001	2780.891	0.581	0.181	8.2E-01

Conventional land-use intensification in low-intensity systems

Small conventional intensification efforts in low intensity systems (e.g. a low increase of stocking density in extensive grasslands) did not show any clear effect on yield or species richness (Figure 2a). A further intensification (from low to medium intensity, e.g. introducing low-input fertilization in a pasture system) resulted in significantly negative effects on species richness (-7.7% [-13.7, -1.3], n=70) without benefitting yields on average (+6.0% [-5.0, +18.3], n=37). When increasing land use intensity from low-intensity systems to become a high-intensity system (e.g. changing a manually worked field to a highly mechanized agricultural system), the mean effect on species richness was negative although non-significant (-12.1% [-25.2, +3.4], n=31), and there was a significant positive effect on yield (+28.8% [+7.5, +54.3], n=14).

Conventional land-use intensification in medium-intensity systems

Conventional intensification within medium-intensity systems (medium-medium) was associated with the most pronounced increases in yields (+84.9% [+65.8, +106.1], n=19) and greatest losses of species richness (-22.9% [-28.1, -17.4], n=29).Yield gains were significant but lower when intensification was carried out from medium to high intensity (medium-high; +24.3% [+11.6, +38.5], n=39). At the same time, species richness showed no significant response to intensification but a negative trend was identified (medium-high; -6.3% [-12.3, +0.2], n=81).

Conventional land-use intensification in high-intensity systems

Conventional intensification within systems already at high intensity (high-high) resulted in smaller, yet significant, increases in yield (high-high; +15.2% [+3.1, +28.7], n=39), while there was a negative, but not significant effect on species richness (high-high; -6.1% [-12.5, +0.8], n=65; Figure 2; Appendix S8).

Species groups, product types and other covariates

Overall, animal species were not significantly affected by higher land-use intensity while plants were (invertebrates -6.7% [-17.2, +5.0], n=54; vertebrates -2.9% [-14.4, +10.2], n=57; plants -11.4% [-17.8, -4.5], n=181; Figure 3). Species richness decreased most (-21.2% [-29.9, -11.5], n=59) and production increased most (+33.3% [+7.4, +65.4], n=26) with conventional intensification in crop-production systems. Green fodder systems showed similar trends, albeit the change in yield was not significant (species richness: -12.4% [-21.8, -1.9], n=86; yield: +14.2% [-5.6, +38.2], n=48), whereas in wood-production systems species richness did not respond to intensification (-1.6% [-8.8, +6.2], n=147; Figure 3) though yield increased by 18.6% ([+3.0, +36.6], n=83). Changes in species richness and yield varied significantly depending on the time since first agricultural use but showed no linear trend over time (Figure 4, Appendix S6). Species richness declined most and yields increased least in arid climates, while in the tropics, species richness declined substantially and yields increased relatively little (Figure 4, Appendix S7).

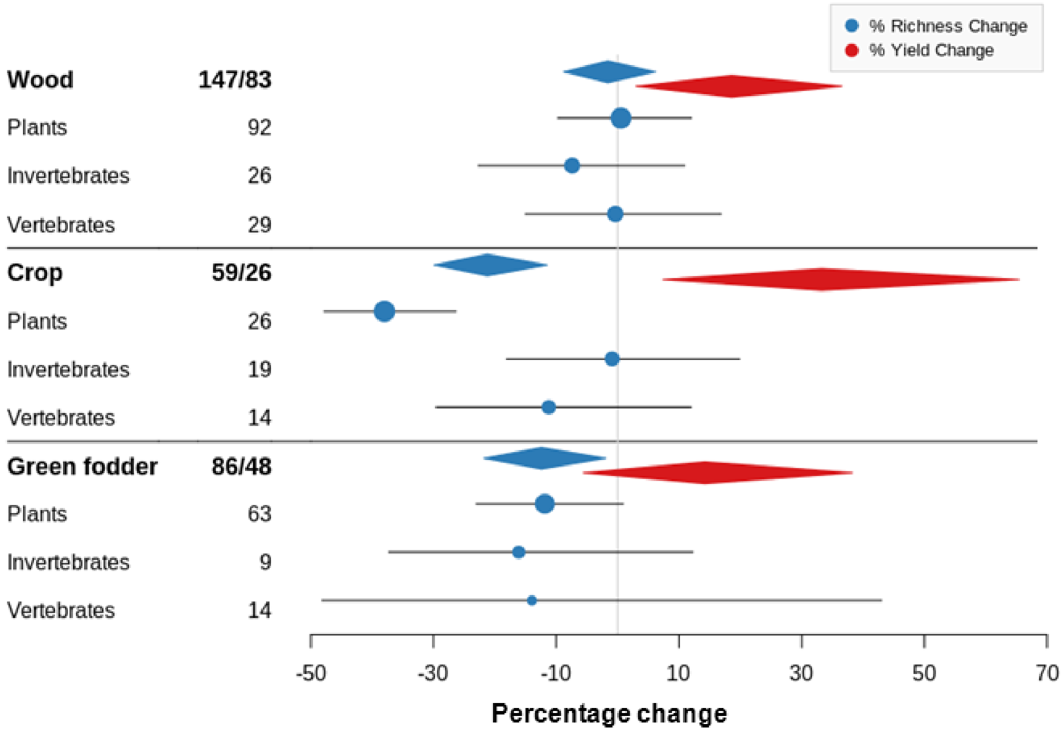


Figure 3 | The effect of conventional land-use intensification on species richness and yield, analysed by product type and species group. Mean percentage change in species richness and yield in response to conventional land-use intensification, for different species groups and product types (1st column). The number of samples (species richness /yield) is shown in the 2nd column. For each species group and product type, the mean across all intensification steps is shown. The impact of species group on yields was not tested. Error bars and horizontal points of the diamonds show 95% confidence intervals. Effect sizes were calculated and analysed as log response-ratios, which were back-transformed and converted to percentage change here.

Results shown are based on 449 cases and are derived from the full models as shown in Table 1a and 1b.

The tested covariates explained a significant proportion of the heterogeneity (Q_M) in effect sizes for both species richness and yield ($p(Q_M) < 0.05$; Table 1). Furthermore, all models that included these covariates showed lower *AICc*, *BIC,* and increased R^2 compared to the null model without covariates. The goodness-of-fit statistic *AICc* suggested that for both species richness and yield the model incorporating all covariates was the most parsimonious model. Furthermore, the heterogeneity statistic, $Q_{M,}$ suggests that a significant amount of heterogeneity was explained in these full models as well.

We found that mean effect sizes did not differ depending on whether species richness and yield were measured from the same species group (t = -0.196, df = 136.85, p = 0.845). However, a significant difference between linked (e.g. when harvesting techniques such as selective logging directly affect the output) and unlinked yield and land-use intensity measures was identified in wood production systems (t = -2.38, df = 42.5, p = 0.022). Pairwise *t*-tests showed no differences in the effect size for different yield units (Mass/area-Area/area p = 0.2, Count/area-Area/area p = 0.12, Count/area-Mass/area p = 0.37).

As the scale dependency of species richness is a well-known constraint for interpreting species richness data in meta-analyses (Chase & Knight, 2013), we tested for scale dependency using the reported size of sampling area. The sampling areas (excluding trap, sweep or observation based methods) ranged from 1 m² (herbaceous plants) to 900 m² (woody plants) in crop studies, from 0.5 m² to 400 m² in fodder studies and from 1 m² (ants) to 3600 m² (small mammals) in forest studies. Linear regression of the mean effect size for species richness as a function of log-transformed sampling area did not reveal a significant relationship ($F_{1,271} = 0.027$, $p = 0.869$; all results are shown in Appendix S9).

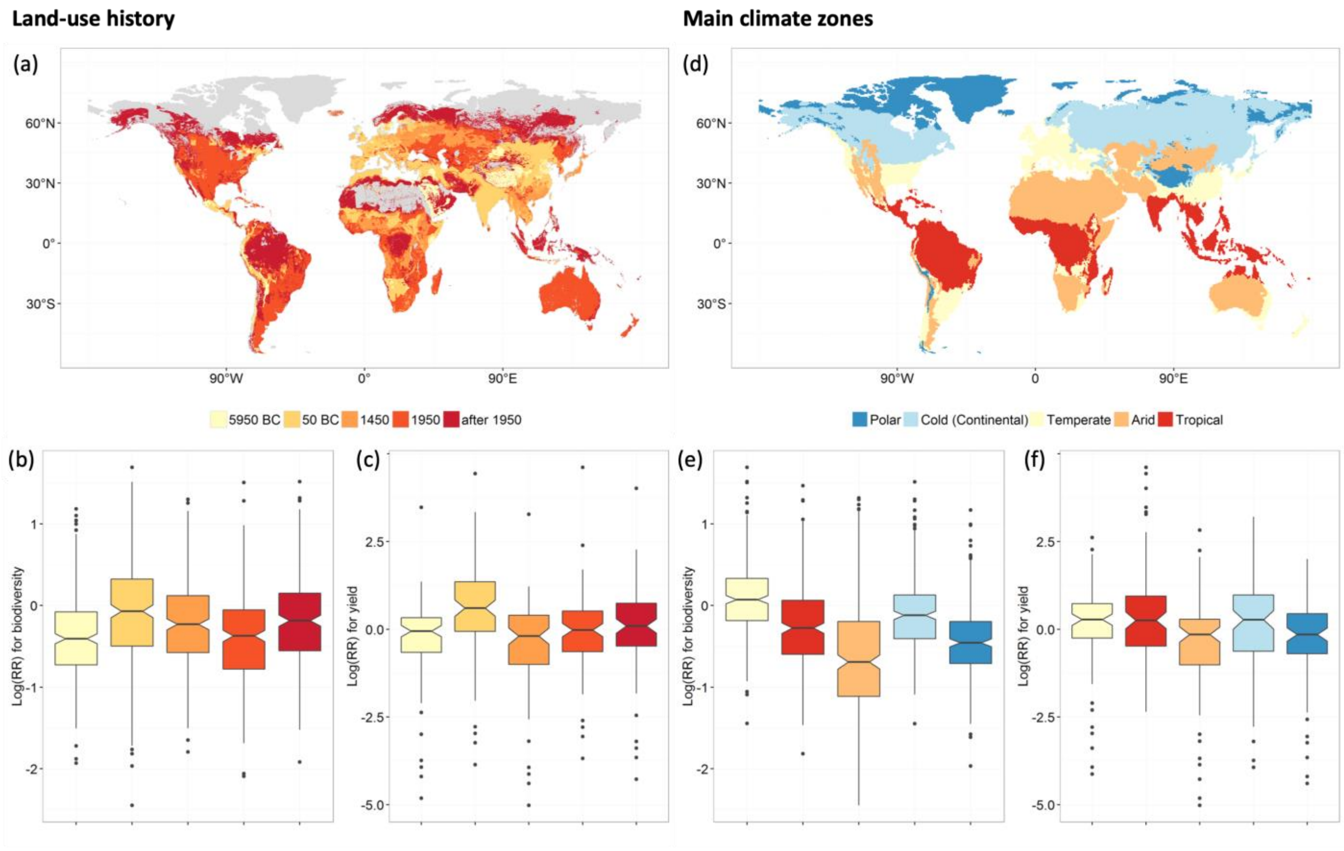


Figure 4 | Analysis of land-use history and climate as explanatory factors. (a-c) Broad classes of land-use history indicating all cells with >20% used area at a given point in time; colours ranging from yellow = areas with longest history of use, to red = areas with shortest history of use. Number of cases included in the analysis per land-use history class (species richness/yield): 5650 BC = 21/9, 50 BC = 115/57, 1450 = 35/23, 1950 = 47/23, after 1950 = 74/36. **(d-f)** Main climate zones according to the Köppen-Geiger climate classification. Number of cases included in the analysis per climate class (species richness/yield): Polar = 2/2, Cold (Continental) = 66/37, Temperate = 178/90, Arid = 4/4, Tropical = 42/24. Notched boxplots **(b,c,e,f)** showing distribution of predicted log-response ratios across individual history and climate classes. Notches are used to compare groups; if the notches of two boxes do not overlap indicates that the medians are significantly different.

Discussion

With this global meta-analysis, we find that there is, on average, a trade-off whereby increases in agricultural/silvicultural yields are accompanied by decreases in species richness when conventional intensification is applied (grand mean in Figure 2). When breaking down these results by the magnitude of intensification steps, species groups and product types, we find that conventional intensification is often successful in increasing yield. However, sub-group analyses also revealed that species richness declines were often not significant, and responses of both species richness and yield were very variable across studies, suggesting considerable scope to optimize the trade-off between agricultural production and biodiversity. For example, we were able to identify situations in which yield can be increased with smaller (i.e. non-significant) losses of species richness. First, species richness in wood production systems shows little to no response to intensification (Storkey et al., 2015; Thomas, 2015), which might be explained by long harvest cycles and the lower disturbance over time needed to manage forests (Paillet et al., 2010). Second, animals are not as negatively affected by intensification as plants which might reflect differences in the overall mobility of some species groups possibly allowing them to mediate the impacts of intensification (Tscharntke et al. 2005). Previous meta-analyses on biodiversity in organic vs. conventional systems support this observation as they show that the biodiversity difference between systems is much higher for plants than for animals (e.g. Bengtsson et al., 2005; Batáry et al., 2010). This vulnerability of plant species to conventional intensification should be taken into account in conservation planning and for ensuring the ecosystem services they deliver. Furthermore, we found no trade-off between production and species richness within low-intensity systems (low-low), where neither yield nor species richness showed notable responses to intensification. These results indicate that, if conventional intensification steps remain small, they have potential to increase production without negative effects on biodiversity. For example, low input systems (e.g. in Sub-Saharan Africa), that have been suggested as candidates for alternative intensification pathways to achieve food security (e.g. Pretty et al., 2018), could potentially undergo low conventional intensification without causing a substantial loss of species. However, in order to provide scientific support to management and policy-making to achieve the dual goal of food production and biodiversity conservation, more research is required. As a first step, upcoming field studies should try to validate the observation that small steps of conventional intensification can increase yield without harming biodiversity by using more robust measures for biodiversity than species richness.

Surprisingly, conventional intensification within high intensity systems (high-high) revealed a non-significant tendency of species richness loss, highlighting that even high intensity systems harbour species that may be lost through further intensification. At the same time, intensification in these systems still leads to significant yield increases, suggesting that production limits have not yet been reached. However, the proportionally lower yield gains within high intensity systems compared to other intensification steps (e.g. low-high, medium-high), indicates that high intensity systems might be approaching such limits (Seppelt et al. 2016). On the contrary, conventional intensification within medium-intensity systems (medium-medium) provides the greatest increase in yields, but is also accompanied by the highest loss of species richness. Consequently, these systems might be the first choice if seeking maximum production increases, but they are also most vulnerable to species richness decline. However, when drawing such conclusions it has to be taken into account that this comparison is based on only 29 richness and 19 yield cases and only one of each is from crop production systems. This highlights that great caution must be taken when interpreting the outcomes of this meta-analysis due to the small number of studies that simultaneously measure yields and biodiversity.

Neither in the grand mean, nor in any of the sub-group analyses (Figure 2, 3), could we identify situations in which conventional intensification increases yield and provides benefits for biodiversity at the same time. Alternative forms of intensification not investigated here, such as ecological or sustainable intensification, may be more suited to uncover these often discussed ‘win-win’ situations (e.g. Fischer et al. 2017a; Seppelt et al., 2017; Bommarco et al., 2018). More holistic approaches that also include social and economic aspects (e.g. profitability) of land-use (e.g. Batáry et al., 2017; Hanspach et al., 2017), may further support the identification of win-win situations and alternatives to conventional intensification. In fact, at an individual level, 71 out of the 292 biodiversity cases in this meta-analysis (extracted from 39 studies) actually show an increase of richness and yield in response to conventional intensification, suggesting that, in some situations, conventional intensification can boost yields while also increasing richness. Most of these cases (43) are extracted from studies in wood production systems (e.g. Summerville et al., 2011), and 14 each from crop (e.g. Batáry et al., 2013) and fodder studies (e.g. Mudrak et al., 2013). Notwithstanding, while these individual examples support the idea that, under certain circumstances, species richness can not only support production but also benefit from conventional intensification, the outcomes of this meta-analysis shall not be used to warrant simplified conclusions but rather provide guidance for directing future research efforts.

Studies on the biodiversity-productivity-relationship have provided evidence that higher biodiversity leads to higher ecosystem productivity (e.g. Seabloom et al., 2017). These outcomes have often been utilized to conclude that biodiversity also benefits the production of biomass actually consumed by humans (e.g. Liang et al., 2016). However, such approaches make the rather unrealistic assumption that people do not care which kind of biomass is harvested (i.e. species identity is irrelevant), whereas most desired products depend on single species. This needs to be considered carefully when drawing conclusions on the benefits ecosystem productivity provides for humans.

Here we used a categorical classification of management intensity to study one specific intensification pathway, i.e. conventional intensification that is based on more intensive use of external inputs. Land management aiming to increase production covers a wide array of management techniques and, therefore, also a wide set of options for management intensification. Previously, authors have argued that management intensity is better captured by the amount of a practice applied instead of a distinction based on management techniques themselves (Erb et al., 2013). However, we here identify a clear lack of studies containing quantitative information on land-use intensification that would allow classifying land-use intensity based on inputs (e.g. mass of fertilizer or pesticides applied), thereby highlighting the need for more studies to report more detailed information on management practices and input quantities in the future. Instead, we used a categorical classification that was capable of incorporating different production systems (crops, fodder and wood) into one intensity gradient. This allowed for a comparison of the effects of yield and biodiversity across widely different contexts and production systems but by focusing mainly on production inputs, this classification also limits this meta-analysis to only study effects of conventional land use intensification. Therefore, this meta-analysis does not allow conclusions on alternative intensification pathways (e.g. ecological or sustainable intensification).

This meta-analysis is no exception to often encountered shortcomings when dealing with the synthesis of data on a global scale (Gerstner et al., 2017) and relies on original studies that usually collect species richness at a single spatial scale and as the only biodiversity measure. However, the magnitude of land use effects on species richness is highly scale dependent and generally increasing with spatial scale (Chase et al., 2018). This is why we cannot entirely rule out that the dependence of species richness on spatial scale does not affect the outcomes presented here, even though we found no effect of spatial grain of the study sites. Furthermore, the relatively small scale at which the synthesized data was originally sampled on (plot size up to 3600 m^2), generally limits the conclusions that can be drawn from this meta-analysis on larger scales. To what degree surrounding areas could have influenced the measurements of richness or yield (e.g. as the source of the local species pool or through providing ecosystem services beneficial for crop production) cannot be disentangled here. By synthesizing species richness, which is still the most widely reported measure of biodiversity (Isbell et al., 2011), we also use an incomplete measure of biodiversity (Pereira et al., 2013), ignoring homogenization effects, a reduction of evenness and the hidden loss of rare or endemic species. Furthermore, species richness is highly dependent on relative abundance of individuals, sampling area and effort (e.g. Gotelli & Colwell 2001), meaning that if a substantial reduction in the number of individuals occurs in response to intensification, it will remain undetected as long as richness is not affected. Similarly, if certain management practices increase the abundance of a few species these become more likely to be sampled, thus increasing measured richness, even though true species richness is not changing at all (e.g. as observed by Crowder et al., 2012). However, only few studies reported on more robust measures of biodiversity (e.g. species abundances, Shannon diversity), alongside yield responses. The fact that a meta-analysis on the Shannon diversity index based on 19 studies and 42 observations does not show any impact of conventional land use intensification on biodiversity (Appendix S10) suggests that biodiversity impacts might depend strongly on the biodiversity indicator examined. Therefore, and because effect sizes are highly confounded by spatial scale (Chase & Knight 2013), achieving synthesis across studies through meta-analysis based on species richness remains problematic.

While the loss of species richness varied depending on the history of land use, we did not find the expected relationship of the time since first agricultural use with the magnitude of species richness loss, providing no evidence that biodiversity had longer time to adapt to human land uses in these areas (Balmford 1996; Perring et al., 2016). Species richness declined most and yields increased least in arid climates, suggesting that these areas are not good candidates for land-use intensification. Again, we caution that by using species richness as a proxy, and by applying a space-for-time substitution approach, potential homogenization and climate change effects could not be considered (e.g. Elmendorf et al., 2015) and the impacts of land-use itself may also be underestimated (França et al., 2016; but see Berg et al., 2015). In addition, response ratios capture only the relative effects of intensification on species richness and yield. This way, changes in absolute values or species identity might be obscured.

A clear caveat to the implications of this meta-analysis for policy or management is that one size does not fit all: in all sub-group analyses, the variation among studies was large. Even where the statistical models explained significant amounts of variation, individual cases may exhibit different outcomes. Identifying the nuances and complexities that make up the intensification-species-richness-production relationship requires a solid foundation of data collected in a globally representative number of different production systems and species groups as suggested by German et al. (2017). As this synthesis has shown, only a comparatively low number of studies have done this so far. Instead, the majority of previous research has focused on the effects of land-use intensification either on biodiversity *or* on yields (Appendix S5; e.g. Newbold et al., 2015; Mauser et al. 2015). It becomes clear that a greater number of studies should aim to gather both types of information on used and non-used land in the future. One way out of this predicament would be the establishment of global, long-term research networks such as has been done with the Nutrient Network (NutNet; Stokstad, 2011).

In a world where human requirements almost always outweigh conservation objectives, one of the major challenges is to identify the form and location of land-use intensification that will best preserve the biodiversity, ecosystem functions, and ecosystem services upon which agricultural production ultimately depends. It is crucial that future studies focus more on areas already used for agriculture or silviculture as these harbour a substantial amount of species which may be lost through intensification. Given the predicted increases in the human population and consumption, it is likely that used land will be intensified further in the near future. It is also likely that even low-intensity systems, such as smallholder farms, which still account for more than 50% of agricultural land globally (Graeub et al., 2016), will turn to conventional intensification in order to boost yields. Here, we provide the first quantitative global synthesis of species-richness-yield relationships in response to conventional intensification in three different types of land use systems. We show that at the current state, the scientific community knows far too little about this relationship to provide well-founded support for policy and management. Although the synthesized findings lack generalizability to larger scales (e.g. regional or landscape scales), we detect multiple conditions in which yield can be increased through conventional intensification without resulting in significant losses in species richness. This suggests that even conventional intensification can in some cases – i.e. if carried out in small steps – result in yield increases without coming at the expense of biodiversity loss. These results should guide future research to understand the circumstances required to achieve such win-no-harm situations in conventional agriculture and explore if such practices could be integrated in alternative pathways of land-use intensification, such as sustainable or ecological intensification.

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