The global distribution of plant species richness in a human-dominated world

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Summary

Human dominance of the Earth's ecosystems has resulted in a dramatic decline of global biodiversity and thereby caused unforeseen changes in ecosystem patterns, processes and functions. A major threat to global biodiversity is anthropogenic land use which includes management and modification of the natural environment. Vascular plants are highly linked to human land-use and are of special importance for all life on Earth. Especially, high plant diversity is needed to maintain ecosystem functions and services and is therefore instrumental to ecosystem health and ultimately human well-being.

In order to halt global biodiversity loss and consequent impacts on human well-being, there have been several international political commitments recently passed (e.g. Convention on Biological Diversity CBD). Their implementation and measure of success depend on good predictions about the current status of biodiversity and its change. However, recent predictions are highly uncertain due to uncertainty in knowledge of current diversity distribution and uncertainty in models. In order to overcome knowledge limitations and improve models, studying ecosystem attributes and their complex interactions with anthropogenic global change, such as land use, is essential and need to incorporate a wider range of spatial scales because: Although land use directly affects ecosystems at local scales, drivers of land-use decisions increasingly act at regional, continental to global scales as a result of globalization, the industrialization of agriculture and forestry, and the increasing influence of transnational cooperations. Moreover, biodiversity loss is of great concern at the regional scale, where the level of endemism is high and usually political decisions about the allocation of conservation funds are made.

The overall aim of this dissertation is to improve predictions about the current status of the diversity of vascular plants and enhance the understanding of how humans have contributed to diversity changes in the past, thereby enabling future predictions. Species richness has been used as an indicator of biodiversity since it is the most widely used measure of ecosystem performance and commonly hypothesized to support ecosystem functioning. A widely used model to predict species richness patterns and changes is the species–area relationship (SAR). It assumes a gradual increase of species richness with increasing sample area and is thus able to make predictions across a range of spatial scales. Yet, previous models used a limited range of model parameters based on theoretical assumptions rather than empirical analyses and assume that human-modified habitat becomes completely inhospitable, ignoring that many species may persist. To adequately predict species richness and its change due to land use it is crucial to obtain a good model fit and to consider the potential of human-modified habitat to sustain species.

For the analysis of the distribution of plant species richness the best available global species richness data for vascular plants has been used. This data contains species richness information within geographical units largely differing in size and shape and has been derived from floras, checklists and other literature sources and thus likely reflect native species richness rather than the current situation including recently introduced species and recent species extinction. Using this data it has been shown that the use of a global SAR with canonical parameters is overly simplistic and does not capture the observed species richness gradient and that accounting for geographical variation in species–area relationships considerably improves the prediction of plant species richness at the global scale. Particular results show that biomes are the most important determinant of species–area variation and therewith suggest that ecosystem productivity and evolutionary history, both aspects captured in biomes, mainly determine the patterns of plant species richness at the global scale.

Plant diversity is globally threatened yet evidence from numerous case studies at regional and local scales is mixed. Much of the current disagreement comes due to the variety of land-use options being examined in various regions and at various temporal and spatial scales, hampering direct comparisons of studies. Furthermore, land-use effects extend beyond the boundaries of transformed land by altering habitat characteristics and thus indirectly affects remaining native vegetation; and specific effects might generally depend on the environmental, historical and socio-economic context. Using a meta-analytic framework and a global dataset extracted from 375 studies the effects and their variation of 11 classes of land use were studied. The analysis unequivocally demonstrates that land use matters, both negatively and positively, but that its effects on plant species richness generally vary depending on the specific type and location of land use.

Recent models of environmental change include land use as equivalent to habitat loss and thereby ignore the conservation value of the countryside. The countryside SAR, as a modification of the classic SAR, consider the conservation value of the countryside, yet have been only applied at small scales where sampled data or atlas data were available. As such data is scarce at continental scales, a countryside SAR which integrates both environmental variation as well as land use into models of biodiversity distribution was presented and tested at the example of Europe. Overall, this countryside-SAR approach overcomes the unrealistic assumptions of previous model approaches about constant or general negative effects of land use. Moreover, integrating varying land-use effects into a SAR-model enable predictions about the combined effects of land use and hence give a much more spatially nuanced picture than the classic SAR-model. Finally, the suggested use of biome-specific SAR parameters also enable to include climate change effects in predictions of biodiversity change. The methodological crux of this study was to combine findings from a global SAR-study and from a meta-analysis in order to parameterize the model.

Despite limitations and remaining challenges in modelling species richness patterns and its changes, this thesis contributes to a deeper understanding of species–area relationships and how patterns of species richness across spatial scales are driven by land use and suggests a model to predict species richness pattern of vascular plants that overcomes limitations of previous models which have served as baseline for global assessments (e.g. Millenium Ecosystem Assessment). Moreover, it provides suggestions how the presented countryside-SAR model can be further improved.

Zusammenfassung

Die menschliche Vorherrschaft auf der Erde hat zu einem drastischen Biodiversitätsverlust geführt und damit zu unvorhergesehenen Veränderungen in Ökosystemstrukturen, -prozessen und -funktionen. Eine der Hauptursachen des globalen Biodiversitätsverlusts ist Landnutzung, was sowohl das Management als auch die Modifizierung von natürlicher Vegetation umfasst. Pflanzen sind demnach stark beeinflusst von Landnutzung und gleichzeitig von speziellem Nutzen für alles Leben auf der Erde. Besonders essentiell ist Pflanzenreichtum für den Erhalt von Ökosystemfunktionen und -dienstleistungen und somit maßgeblich für die Gesundheit der Ökosysteme und letztlich auch für das menschliche Wohlergehen.

Um den globalen Biodiversitätsverlust aufzuhalten, wurden zuletzt zahlreiche internationale politische Verpflichtungen verabschiedet (z.B. die Convention on Biological Diversity CBD). Deren Umsetzung und die Auswertung von getroffenen Maßnahmen sind abhängig von Vorhersagen zum gegenwärtigen Stand der Biodiversität und deren Veränderungen. Existierende Vorhersagen sind allerdings sehr ungenau aufgrund von unzureichendem Wissen über die aktuelle Verteilung von Biodiversität und Unsicherheit in den Vorhersagemodellen. Es ist daher wichtig, Ökosystemeigenschaften und deren komplexe Zusammenhänge mit Landnnutzung zu untersuchen und dabei eine große Bandbreite räumlicher Skalen zu betrachten: Auch wenn Landnutzung Ökosysteme direkt nur lokal beeinflusst, so werden verschiedene politische Entscheidungen auf regionaler, kontinentaler und zunehmend auf globaler Ebene getroffen, die wiederum lokale Landnutzungsentscheidungen bestimmen. Darüberhinaus, ist Biodiveritätsverlust auf regionaler Ebene besonders dramatisch, weil viele Arten nur regional beschränkt vorkommen, weshalb auch auf regionaler Ebene Naturschutzplanungen stattfinden.

Die übergeordneten Ziele dieser Arbeit sind, die Vorhersagen zum gegenwärtigen Stand der Pflanzendiversität zu verbessern und das Verständnis für den menschlichen Beitrag zu vergangenem Biodiversitätsverlust zu erweitern und in zukünftige Modellvorhersagen zu integrieren. Als Indikator für Biodiversität wurde Artenreichtum betrachtet, da dies ein gängiges Maß für Ökosystemverhalten ist und gemeinhin vermutet wird, dass es die Bereitstellung von Ökosystemdienstleistungen unterstützt. Ein weit verbreitetes Modell zur Vorhersage von Artenreichtum und dessen Veränderung ist die

Art-Areal Beziehung (engl.: species–area relationship SAR), das annimmt, das Artenreichtum mit der Untersuchungsfläche zunimmt. Damit ist es möglich, über eine große Bandbreite räumlicher Skalen Vorhersagen zu machen. In der Vergangenheit wurden jedoch sehr vereinfachende Annahmen zu dem Modell getroffen und nur ein begrenztes Set an Parametern benutzt, die zwar theoretisch aber nicht empirisch fundiert waren. Um adeqate Vorhersagen zu Artenreichtum und dessen Veränderung zu machen ist es deshalb unabdingbar, ein gutes Modell zu fitten und das Potential von menschenveränderten Habitaten zur Beherbergung von Arten zu berücksichtigen.

Für die Analyse der globalen Verteilung von Pflanzenreichtum wurde der bislang umfangreichste globale Datensatz benutzt. Dieser Datensatz beinhaltet Daten zu Artenreichtum in Abhängigkeit von Gebietsgrößen und basiert auf Floren, Checklisten und anderen Literaturquellen. Somit beschreiben die Daten eher die natürliche Vegetation als die aktuelle mitsamt den gebietsfremden Arten und den jüngsten Artverlusten. Anhand dieser Daten konnte gezeigt werden, dass ein globales Art-Areal Modell zu vereinfachend ist und Vorhersagen verbessert werden, wenn Modellparameter zwischen geografischen Regionen variieren können. Insbesondere wurde gezeigt, dass Biome wichtigster Faktor zur Erklärung, der Art-Areal-Varianz ist, was darauf hinweist, dass besonders Ökosystemproduktivität und evolutionäre Geschichte für die globale Verteilung von Pflanzenreichtum verantwortlich sind.

Pflanzendiversität ist zwar global gefährdet, Fallstudien auf regionaler und lokaler Skala jedoch berichten von gemischten Beobachtungen. Viele der beobachteten Unterschiede sind auf die Vielzahl von Landnutzungsoptionen zurückzuführen, die in verschiedenen Regionen und auf unterschiedlichen zeiltichen und räumlichen Skalen untersucht werden und welche einen direkten Vergleich von Studien zu Landnutzungseffekten erschweren. Darüberhinaus, hat Landnutzung auch über die Grenzen von genutztem Land einen Effekt auf Habitateigenschaften und damit indirekt auf den Artenreichtum der übrigen natürlichen Vegetation; und im Allgemeinen dürften Effekte von Umweltbedingungen und dem historischen und sozio-ökonomischen Kontext abhängen. Um die Effekte und deren Varianz von 11 Klassen von Landnutzung zu untersuchen, wurde ein globaler Datensatz basierend auf 375 Fallstudien erstellt und metaanalytische Methoden angewandt. Die Analyse zeigt eindeutig, dass Landnutzung signifikante Effekte auf Pflanzenreichtum hat, sowohl negativ als auch positiv, jedoch allgemein von der Landnutzungsklasse und dem Ort abhängen, wo Landnutzung stattfindet.

Aktuelle Umweltveränderungsmodelle berücksichtigen Landnutzung als Äquivalent zu Habitatverlust und ignorieren dabei, das auch menschveränderte Landschaften einen Naturschutzwert haben. Das 'Countryside SAR'-Modell berücksichtigt diesen Wert, wurde jedoch bisher nur auf kleinere räumliche Skalen angewandt, wo genauere Daten zu Artverteilungen vorliegen. Da solche Daten für größere Regionen oder gar global nicht zur Verfügung stehen, wird ein Ansatz präsentiert und anhand Europas implementiert, der sowohl Umweltvariabilität als auch Landnutzung berücksichtigt. Damit verzichtet dieses Modell auf die gängige Annahme das genutztes Land keinen oder einen generell niedrigeren Wert im Vergleich zu natÃ¼rlicher Vegetation als Habitat für Pflanzen hat. Darüberhinaus ermöglicht der Modellansatz die kombinierten Effekte von unterschiedlichen Landnutzungsklassen auf Pflanzenreichtum zu untersuchen und gibt somit ein räumlich differenzierteres Bild als das klassische Art-Areal Modell, welches Landnutzung unberücksichtigt lässt. Die Benutzung von biom-spezifischen SAR-parametern erlaubt zusätzlich die Vorhersage von Klimaeffekten auf die Verteilung von Artenreichtum. Methodisch fungiert das hier präsentierte 'Countryside SAR'-Modell als Synthese der globalen SAR-Studie und der Meta-Analyse, deren Ergebnisse genutzt werden, um das Modell zu parametrisieren.

Abgesehen von den Beschränkungen und bleibenden Herausforderungen die Modellierung der Verteilung von Artenreichtum und dessen Änderung betreffend, trägt die vorliegede Arbeit zu einem tieferen Verständnis von Art-Areal Beziehungen bei und auch wie Artenreichtum über große Bandbreite räumlicher Skalen von Landnutzung beeinflusst wird. Darüberhinaus, wird ein Modell präsentiert, was die Verteilung von Artenreichtum von Pflanzen voraussagt und durch die Integration von Landnutzung und dessen vielfältige Effekte eine deutliche Verbesserung gegenüber existierenden Modellen darstellt, die bisher für globale Bewertungen verwendet wurden (z.B. das Millenium Ecosystem Assessment). Abschließend werden Vorschläge gemacht, wie das präsentierte 'Countryside SAR'-Modell weiter verbessert werden kann.

CHAPTER 1

Introduction

Unlike any other species humans have shaped the face of the Earth (Ellis, 2015). They transformed landscapes and ecosystems in ways that enhance food, timber, fibre and fuel production. Land transformation encompasses a wide variety of activities that vary substantially in their intensity and consequences. Estimates of the fraction of land transformed or degraded by humanity fall in the range of 39 to 50% (Vitousek *et al.*, 1997). Moreover, remaining natural land often has been divided into fragments by human alteration of the surrounding areas. This fragmentation affects the species composition and functioning of otherwise little modified ecosystems. Thereby the effects of land transformation extend beyond the boundaries of transformed lands (Vitousek *et al.*, 1997).

Most of these changes resulted in the loss of biodiversity. Biodiversity, i.e. the variety of genes, species and ecosystems, however, is essential for ecosystem functioning and services which are fundamental for human well-being (Daily, 1997; Cardinale *et al.*, 2012). As a driver of biodiversity loss human-induced environmental changes caused unforeseen changes in ecosystem patterns, processes and functions. Especially the exceeding rate of species extinctions (Pimm *et al.*, 1995; Millenium Ecosystem Assessment, 2005) and the homogenization of the distribution of species on Earth (McKinney & Lockwood, 1999) is of great concern for human society.

In order to ultimately halt the loss of biodiversity, international conventions seek to monitor and predict changes in biodiversity (e.e. Convention on Biological Diversity CBD[1]). Predictions about the rate of biodiversity loss require both assessments of the current status and future predictions. Therefore, expanding our understanding of ecosystem attributes and their complex interactions with anthropogenic global change, such as land use, is essential and need to incorporate a wider range of spatial scales because: Although land use directly affects ecosystems at local scales, biodiversity loss is of great concern at the regional scale, where the level of endemism is high and usu-

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[1] https://www.cbd.int/

ally decisions about external factors, e.g. subsidies, and the allocation of conservation funds are made (e.g. EU CAP, NATURA2000). Moreover, the drivers of land-use change increasingly act at continental to global scales as a result of globalization, the industrialization of agriculture and forestry, and the increasing influence of transnational cooperations, NGOs, and institutions (Lambin & Meyfroidt, 2011; Meyfroidt *et al.*, 2013). As many land-users are influenced by these broad-scale drivers in similar ways, the collective impact of local land-use change at broader scales can be very large.

1.1 Land use

In the context of biodiversity loss, land use (and precedent land-cover change) is considered as the major threat, greater than those of any other component of global change such as increasing atmospheric carbon dioxide, nitrogen deposition, climate change, and biotic exchange (Fig. 1.1, Vitousek, 1994; Sala *et al.*, 2000; Millenium Ecosystem Assessment, 2005).

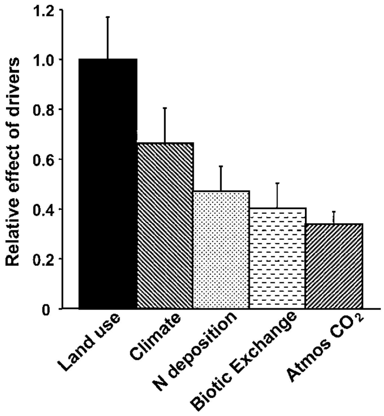

Figure 1.1: Relative effect of major drivers of biodiversity change. Values are averaged across biomes relative to the maximum change, which resulted from change in land use. Thin bars are standard errors and represent variability among biomes. Source: Sala *et al.* (2000)

It is important to distinguish between land use and land cover. While land cover describes the terrestrial surface, land use has been defined as the purposes for which human exploit the land cover (Lambin & Geist, 2006). However, land-use decisions involve management within and transitions between land-cover types. As such land cover and land use are intimately linked. Land-cover changes constitutes immediate changes of the attributes of terrestrial surface, including vegetation structure, actual and potential primary productivity and soil quality and are visible in remotely-sensed data (Lambin & Geist, 2006). Land use changes ecosystems more subtle via land transformation, including modification, fragmentation, and intensification (e.g. through fertilization) and can be inferred from remotely-sensed data under some circumstances or from groundbased analysis (Lambin & Geist, 2006; Fischer & Lindenmayer, 2007). A comprehensive and uniform framework about land-use types and inherent dynamics would be useful for the systematic analysis of its consequences for the environment, yet is still lacking. Lambin & Geist (2006) proposed a very simplistic illustration of land-use/cover states and possible transitions in the tropics (Fig. 1.2) which might serve as a vantage point for a global framework.

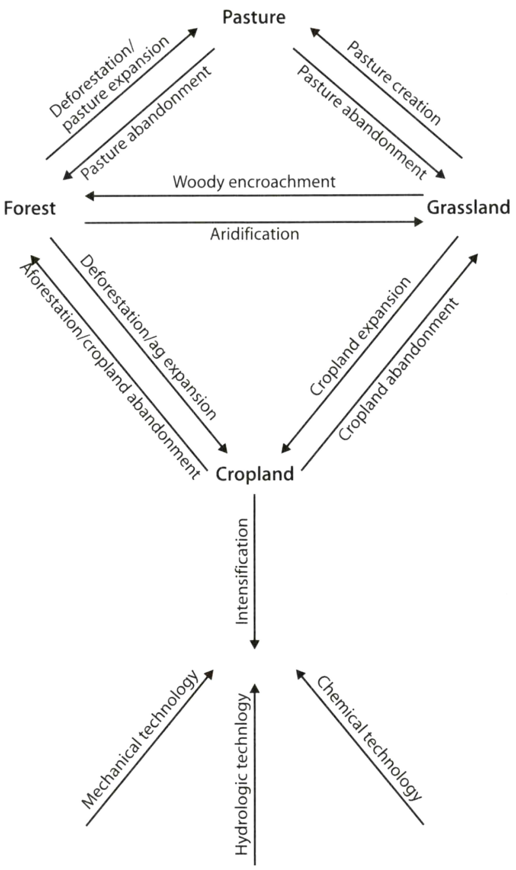

Figure 1.2: Framework of potential transitions between land-use/cover states. Source: Lambin & Geist (2006)

The historical and current distribution of used land worldwide shows large regional differences (Ellis *et al.*, 2013). While industrial countries historically experienced large ecosystem transformation, land transformation in developing countries is rather recent. This pattern occurs because globalization has increased connectivity between world regions (Lambin & Meyfroidt, 2011; Ellis *et al.*, 2013; Meyfroidt *et al.*, 2013). Regions having the highest demand for land resources displaces their production needs to less developed countries where production costs are less (Meyfroidt *et al.*, 2010; Ellis *et al.*, 2013; Meyfroidt *et al.*, 2013). As a result large areas in industrial countries are becoming abandoned and reforested (Navarro & Pereira, 2012; Munroe *et al.*, 2013) while large proportions of mature tropical forest in developing countries are becoming deforested and transformed to cropland (Meyfroidt *et al.*, 2010, 2013).

In general, land use directly affects biodiversity by the reduction of habitat area and habitat diversity, and leads to new environmental conditions and habitats. Thereby land use alters species diversity directly by removing and introducing species and altering their rates of reproduction or mortality, and indirectly by altering species interactions, modifying the carrying capacity of the habitat, lowering resource abundance and availability needed for species vigor (Walker, 2012). In addition, land use indirectly affects habitat characteristics linked to species diversity, such as area and age, not only of the managed land but also of remaining natural land within the same matrix. As such, a matrix-approach which considers the collective impacts of land use within the same matrix is highly valuable.

1.2 Plant diversity

Vascular plants[2] are of special importance for all life on Earth. As main primary producer in terrestrial ecosystems they form the basis of the terrestrial food chain, and are the principal structural elements of ecosystems. Thereby they are highly associated with the total diversity of all living organisms (Nic Lughadha *et al.*, 2005; Qian & Ricklefs, 2008). As such, vascular plants have been used as primary criterion to deliminate biodiversity hotspots for conservation priorities (Myers *et al.*, 2000). Moreover, high plant diversity is needed to maintain ecosystem functions and services and is therefore instrumental to ecosystem health and human well-being (Quijas *et al.*, 2010; Isbell *et al.*, 2011; Cardinale *et al.*, 2012; Lange *et al.*, 2015).

The group of vascular plants is considered to be well known relative to their size and it is generally agreed that most plant species have already been described (Millenium Ecosystem Assessment, 2005). However, no complete authoritative list of accepted species names exist, exemplified in the large range of recent estimates of seed plant species richness (estimates range from 220,000-400,000, Nic Lughadha *et al.*, 2005). As many plant species are only known from single herbarium specimens the number of species for which range maps exist is unrepresentative of plant diversity more broadly (Nic Lughadha *et al.*, 2005). As a last resource for assessing the current status of plant diversity, overviews of global species richness patterns exist (Mutke & Barthlott, 2005; Kier *et al.*, 2005). Although species richness is not synonymous with diversity, which encompasses both the variation in the number of species and their relative abundances,

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[2] Throughout the term "plant" is used as shorthand for vascular plants

declines in species richness can be an indicator of diversity loss.

Global maps of plant species richness are based on floras, checklists and other literature sources for geographical units representing natural or administrative units, such as countries or protected areas (Kier *et al.*, 2005; Kreft & Jetz, 2007). In order to map species density, i.e. species richness per area, these data are usually projected using species–area relationships.

1.3 Species–area relationships

The species–area relationship (SAR) is a prominent concept for predicting species richness and biodiversity loss and therefore has profound importance for conservation biogeography (Ladle & Whittaker, 2011). This model assumes an increase in species richness with increasing sample area and is mostly approximated by a power law or a linear curve in the log–log space (Arrhenius, 1921) because it has been shown to describe SARs appropriately under most conditions (Connor & McCoy, 1979; Dengler, 2009; Triantis *et al.*, 2012):

$$S = c \cdot A^z \tag{1.1}$$

or its linear function in the log–log space:

$$\log(S) = \log(c) + z\log(A) \tag{1.2}$$

The intercept c can be interpreted as the average number of species per unit area (e.g. $A = 1$), and z describes the slope of the log–log relationship.

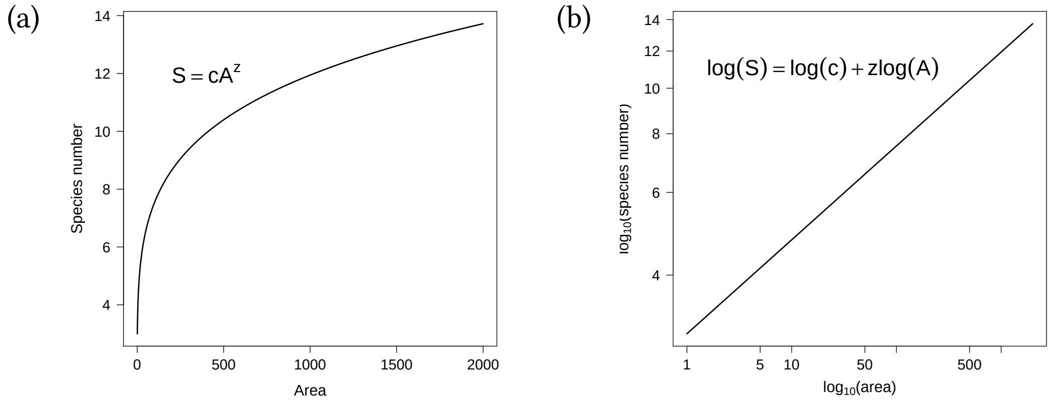

Figure 1.3: Representation of the species–area relationship modeled by a power law. (a) in original space, (b) in log–log space

Species loss is estimated as the difference in species richness after a particular loss of habitat area. The proportional reduction of species, often called extinction rate, is particularly determined by the slope of the curve. Therefore, it is of particular importance how the slope of the SAR is quantified. However, recent estimates of species loss are flawed by the common assumption of a universal slope of this curve, typically ranging from 0.15 to 0.25 or 0.35 (e.g. Pimm *et al.*, 1995; Brooks *et al.*, 2002; Thomas *et al.*, 2004). The use of these restricted values is based on several theoretical assumptions (Preston, 1962; Harte & Kitzes, 2012), but lack empirical validation. Actually, it is likely that the parameters of the model systematically vary depending on a range of properties such as spatial scale, taxon, regional richness, and sampling design (Scheiner, 2003; Turner & Tjørve, 2005; Whittaker & Matthews, 2014).

Recently, a debate arose whether SARs are the most appropriate method to estimate extinction rates (He & Hubbell, 2011; Pereira *et al.*, 2012). As an alternative the endemic–area relationship (EAR) has been proposed which counts species only if the entire species range is within the sampled area (in contrast, the SAR counts species by their first appearance). This debate shows that SARs are based on several simple assumptions which might not be met in reality:

- **Distribution of species**
  SARs assume a general increase in species number with increasing sample area. A species is counted when sample area partly overlaps with the species range. In contrast, a species is lost if sample area overlaps the entire species range, i.e. the species is endemic to the habitat lost. Only if species are randomly distributed, the expected area at which the first individual of a species is encountered while enlarging the sampling area is exactly the same area where one would find the last individual of a species while decreasing sampling area. However, in case of aggregated species, He & Hubbell (2011) claim that extinction rates from SAR are always overestimated.

- **Geometry of habitat loss and scale**
  Pereira *et al.* (2012) argued against He & Hubbell (2011) that extinction rates from SAR are always overestimated. They showed that the reliability of extinction rates depend on how habitat is lost because both methods, SAR and EAR, estimate endemic richness of an area although of different geometry. If habitat loss occurs in the periphery, it is SAR that describes extinction rates because it approximates the number of endemics in outer rings towards the centre of the plot, the inward EAR. Hence, extinction rates from SAR are a good approximation of the inward EAR as long as the SAR data points fit the power law. However, this fit depends on the scale of the SAR. At very small scales for instance, several studies have shown that the SAR is rather curvilinear in log–log space.

- **Landscape composition and the suitability of human-modified habitat** Another source of uncertainty in estimating future extinction rates includes the assumption that a habitat becomes completely inhospitable, ignoring that many species persist in human-modified habitats. Therefore, different approaches has been suggested (Tjørve, 2002; Triantis *et al.*, 2003; Pereira & Daily, 2006; Koh & Ghazoul, 2010) that consider both, habitat diversity and habitat area to explain species richness patterns.

The debate about the application of SARs to adequately estimate species richness and its change highlight two important considerations in future studies: First, it is crucial to obtain a good model fit between species richness data and area and second, to consider the potential of human-modified habitat to provide high-value habitat for species.

1.4 Research questions

There is considerable concern that biodiversity is lost at unprecedented rates causing irreversible changes in ecosystem processes, functions and services humans depend on. Therefore, understanding how humans contribute to biodiversity changes, most important by land use, is crucial to understand, predict, and successfully manage ecological pattern, process, and change.

The overall aim of this dissertation is to improve predictions about the current status of biodiversity and enhance the understanding of how humans have contributed to biodiversity changes in the past, thereby enabling future predictions. Vascular plants have been used because this group of species is of particular importance for ecosystems and highly linked to human land use. Species richness has been used as an indicator of biodiversity since it is the most widely used measure of ecosystem performance and commonly hypothesized to support ecosystem functioning (Hooper *et al.*, 2005; Isbell *et al.*, 2011). The species–area relationship has been explored as a model to predict species richness depending on the available habitat. Despite the awareness of its simplistic assumptions about species distributions and the geometry of habitat loss, its methodological development is highly important. Especially, the last point of criticism about the consideration of habitat diversity and the suitability of human-modified habitat can be resolved. Therefore the main questions of this dissertation are:

1. **Distribution of native plant species richness at the global scale** – A key step to apply SARs to predict species richness and its loss is to accurately estimate the slope of the relationship, but researchers typically apply only one global (canonical) slope. Can we improve a global SAR model to estimate the distribution of native plant species richness at the global scale by inducing variation due to historical or environmental determinants?

2. **Effects of land use on plant diversity** – Land use is considered as major threat to global plant diversity yet how does this relates to smaller spatial scales? How do different types of land use affect plant diversity at local to regional scales and does these effects further depend on the environmental, historical or socio-economic context?

3. **Integrating land use into broad-scale species richness pattern using a countryside SAR approach** – Previous SAR-models consider land use as equivalent to habitat loss. How can we integrate the varying effects of land use into a SAR-model which predict the distribution of native plant species richness?

Chapter 3 contains three manuscripts, two of which have been published in scientific journals as part of this dissertation and the third one is close to submission. The three manuscripts are directly linked to the three research questions from above: Manuscript 1 adresses question 1 and study how incorporating geographic variation into SARs improves predictions of global species richness patterns. Manuscript 2 adresses question 2 and synthesizes case-study findings about the varying effects of land use on plant species richness. Manuscript 3 adresses question 3 and make use of the findings from the previous research questions. Chapter 4 summarizes findings in light of the research questions, discusses remaining challenges and limitations, and ultimately the importance of the findings for policy and research.

CHAPTER 2

Concept and Methods

2.1 The classic species–area relationship

The species–area relationship (SAR) is a prominent concept for predicting species richness and biodiversity loss. A key step in defining SARs is to accurately estimate the slope of the relationship, but researchers typically apply only one global (canonical) slope, typically ranging from 0.15 to 0.25 or 0.35 (e.g. Pimm *et al.*, 1995; Brooks *et al.*, 2002; Thomas *et al.*, 2004). The use of these restricted values is based on several theoretical assumptions (Preston, 1962; Harte & Kitzes, 2012), but is not empirically validated. Other researchers suggest that the parameters of the model will systematically vary depending on a range of properties such as spatial scale, taxon, regional richness, and sampling design (Turner & Tjørve, 2005; Scheiner, 2003; Whittaker & Matthews, 2014).

2.2 Accounting for geographical variation in global species–area relationships

The first chapter of this thesis aims to illustrate that the classic SAR approach is overly simplistic in its use of global parameters and investigated how geographically varying determinants of SARs affect SAR-parameters and species richness estimates of vascular plants at the global scale.

To examine the effects of different determinants of SAR variation, globally distributed species richness data of vascular plants have been used. Data contains species richness information within 1032 geographical units differing in size (areas ranged between 10^1 to $6x10^5$ km^2) and shape, representing natural or administrative units, such as countries or protected areas (Fig. 2.1, for details see Kier *et al.*, 2005; Kreft & Jetz, 2007) and has been derived from floras, checklists and other literature sources. For the analysis oceanic islands were excluded because isolation and geology dominate species richness patterns there (Rosenzweig, 1995; Whittaker & Fernández-Palacios, 2007; Kreft & Jetz, 2007). Although large gaps existed in the data (e.g. Brazilian Amazon), the data set covered almost the full spectrum of global variation in abiotic conditions.

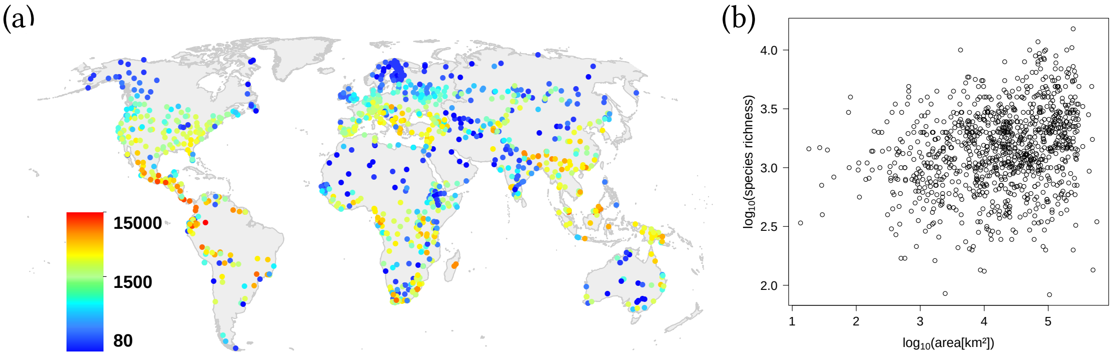

Figure 2.1: (a) Geographic distribution of richness data used in the analysis (after Kreft & Jetz (2007). Dots present centres of geographical units. Regions differ in size, and species counts have not been standardised; (b) Observed relationship of log species-richness against log area. Source: Gerstner *et al.* (2014a)

The number of species in a given area A of known composition can be estimated by summing up species richness estimates for each class of determinant (e.g. biomes) assuming a minimum overlap in species:

$$\log_{10} S = \sum_i (\log_{10} c_i + z_i \log_{10} A) \cdot \%R_i \tag{2.1}$$

where i denotes the classes, i.e. c_i, z_i are SAR parameters and $\%R_i$ is the percentage area covered by the corresponding class of determinants (e.g. biomes), and $\sum_i \%R_i = 1$.

Moreover, estimating extinction rates using the classic SAR is based on the assumption that human-modified habitat is completely lost, i.e. becomes completely inhospitable, ignoring that many species persist in human-modified habitats. Hence, it is important to include other variables related to environmental heterogeneity within sampling units. Therefore, different approaches have been suggested (Tjørve, 2002; Triantis *et al.*, 2003; Pereira & Daily, 2006; Koh & Ghazoul, 2010) which are applicable to include various responses of species groups to landscape diversity and land use.

2.3 Accounting for habitat diversity in species–area relationships

The classic SAR considers habitat area, but does not consider landscape patterns that contain more than one habitat type. However, several studies have shown that species richness generally benefit from habitat diversity, including the number of different habitats (e.g. Stein *et al.*, 2014). Beside native habitat, human-modified habitat may contribute to the overall species richness of a landscape because species tolerate or even benefit from multiple habitats (e.g. Desrochers *et al.*, 2011). Therefore, different approaches have been suggested that consider both, habitat diversity and habitat area to explain species richness patterns (Tjørve, 2002; Triantis *et al.*, 2003; Pereira & Daily, 2006; Koh & Ghazoul, 2010). Some of them place a focus on the number of different habitats only while other also consider the response of species to the different habitats in the landscape and thereby are able to consider sensitivity of species richness against habitat change. In the following the different approaches are explained and discussed.

Multi-habitat species–area curves (Tjørve, 2002)

This approach builds models of species diversity in multi-habitat landscapes by combining species–area curves for different habitats. The main idea is to sum up the number of species found in different habitats and to subtract the number of species overlapping between two or more habitats. However, for the consideration of more than two habitats it a constant species overlap between habitats is assumed. The Tjørve (2002) model predicts which habitat composition (size and numbers) would maximize the number of species depending on their contribution to overall species richness. Tjørve (2002) further discusses the applicability of his model for defining nature reserves. Although Tjørve (2002) bases his rather conceptual explanations on the exponential function $S = z \cdot \log(1 + A)$ for one habitat,[1] his explanations could be applied to other SAR functions as well.

Choros Model (Triantis *et al.*, 2003)

Triantis *et al.* (2003) proposed to account for the number of different habitat types in the classic SAR. Instead of using area only, they proposed the use of the product of area and number of habitats within this area. This term $K = H \cdot A$ is called choros. The species richness of the region is then expressed as a power function of the choros

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[1] In contrast to the original exponential function, Tjørve (2002) substituted $logA$ with $log(1 + A)$ in order to overcome the inherent problem of S having no value at $A = 0$ in the original model.

K:

$$S = c \cdot K^z. \tag{2.2}$$

In contrast to Tjørve (2002), Triantis *et al.* (2003) compared the quality of the fit of their model with the power SAR using species richness data of insular biotas (from island and mainland ecosystems). They found that in twenty of twenty-two studied datasets their choros model outperform the classic power SAR and that z-values in the choros model tend to be lower. For implementation of the choros model, discrimination of habitat is crucial and should be based on the natural history of the taxon studied which will allow comparisons among different studies.

Countryside species-area relationships (Pereira & Daily, 2006)

Pereira & Daily (2006) proposed a countryside SAR that accounts for the conservation value of transformed habitat by introducing a parameter h_i reflecting the habitat affinity of a species group to habitat type i, i.e. proportion of area that can be effectively used by the species group:

$$S = c \cdot (\sum_i h_i A_i)^z \tag{2.3}$$

Matrix-calibrated species-area relationships (Koh & Ghazoul, 2010)

Similarly, Koh & Ghazoul (2010) highlight the importance of considering the effects of landscape matrix when estimating species loss based on SARs. Koh & Ghazoul (2010) proposed a matrix-calibrated SAR within which the z-value of the power model (eqn. 1.1) can be partitioned into two components: γ, a constant, and σ, a measure of the sensitivity of the taxon against habitat transformation (quantified as the proportional increase or decrease in the number of species so that $0 < \sigma < \infty$):

$$z = \gamma \cdot \sigma. \tag{2.4}$$

In contrast to previous models this model is specifically proposed for estimating species loss after habitat transformation rather than species richness within a matrix:

$$\frac{S_{new}}{S_{orig}} = (\frac{A_{new}}{A_{orig}})^{\gamma \cdot \sigma} \tag{2.5}$$

Hence, this model basically assumes that some habitat gets immediately lost, e.g. through urban transformation, so that $A_{new} < A_{orig}$. However, if zero habitat within a matrix is completely lost, species richness would not change (cf. their example and the case

East Melanesian islands). Although this model is certainly useful in some situations we can think of many situations where this assumption leads to unrealistic zero estimates of species loss.

Comparison of approaches and conclusion

The multi-habitat species–area model (Tjørve, 2002) mainly consists of conceptual considerations and has not yet been implemented or empirically compared to other model approaches. Yet simple in the two-habitat case, it gets more and more complicated if more habitats are considered and one wants to surrender the simple assumption of constant species overlap between habitats. Recent studies have shown that the countryside SAR is superior to both the matrix-calibrated SAR (Pereira *et al.*, 2014) and to the choros model (Proença & Pereira, 2013) in explaining diversity pattern in countryside landscapes. So far, these improved models have only been applied to selected taxa and small regions (e.g. Proença & Pereira, 2013). Developing these models further enable us to quantify the impact and trade-offs of land-use effects on biodiversity between different plausible land-use scenarios.

The countryside SAR accounts for the conservation value of transformed habitat by introducing a parameter for habitat affinity to a certain land-use type, i.e. the proportion of area that can be effectively used by the species group. In order to estimate the habitat affinity of vascular plants towards land use at a local to regional scale we undertook a quantitative synthesis using meta-analytic techniques.

2.4 Meta-analysis of effect sizes

Meta-analyses are now a commonly used tool in ecology and environmental sciences to quantitatively review a large number of studies on the same topic (e.g. Arnqvist & Wooster, 1995). Thereby statistical methods are employed to combine results and evaluate variation among study findings. In ecology, meta-analyses are used to find and explain general patterns across different taxa and environments.

In ecology the term meta-analysis is mostly associated with meta-analysis of effect sizes (Vetter *et al.*, 2013) while in other scientific fields, e.g. geography, it is used more loosely for various techniques to statistically combine metadata, not necessarily effects (Magliocca *et al.*, 2014). The products of such meta-analyses are quantified effect sizes and their sampling variances, which can be estimated from the data given in the studies.

Basic steps in a meta-analysis of effect sizes include formulating a research question, searching a representative set of relevant studies (reproducible and objective), transforming the outcome of each study into a standardized measure of the direction and magnitude of an effect of interest, and finally combining effect sizes across studies. By accompanying the meta-analysis with a systematic review the whole process becomes rigorous, transparent and repeatable (Koricheva *et al.*, 2013).

2.5 The case study region Europe

Europe is one of few world regions with a very long history of land use leaving few landscapes as natural (Ellis *et al.*, 2013; Kaplan *et al.*, 2009; Stoate *et al.*, 2009). Historically, land management was low intense and has resulted in a rich assemblage of species (e.g. Stoate *et al.*, 2009). Today, about 50% of all species in Europe depend on semi-natural habitats characterized by such low intense management regimes, including a number of endemic and threatened species (Stoate *et al.*, 2009) and most of Europe's native forests, which have been altered by management at some point in recent centuries, are characterized by a more homogeneous tree composition, vertical stratification, and age structure compared to a natural forest (Paillet *et al.*, 2010).
From reconstruction of historical floras it has been estimated that highest plant diversity occurred around 1850 (Poschlod *et al.*, 2005). However, from that period onwards, high land-use pressure resulted in changes in land use which have caused and still causes a decrease in plant diversity in Europe. These threats include (Bengtsson *et al.*, 2000; Poschlod *et al.*, 2005):

- agricultural intensification through fertilization,
- reduced landscape heterogeneity by enlargement of agricultural sites,
- abandonment of less productive sites,
- intensive forest cultivation practices, e.g. planting of monocultures and exotic species in European forests.

Europe is also an intensely studied region where a majority of ecological case studies is located (Martin *et al.*, 2012). Furthermore, large amounts of high quality land-use data are available. Finally, using the Atlas Flora Europaeae (AFE) enable the validation of model predictions. The AFE which covers the geographic extent of Europe though, only covers about 30% of the known European flora, but it has been suggested that the spatial pattern of species richness is representative (Kalwij *et al.*, 2014).

CHAPTER 3

Research Papers

3.1 Accounting for geographical variation in species–area relationships improves the prediction of plant species richness at the global scale

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Gerstner, K., Dormann, C.F., Václavík, T., Kreft, H. & Seppelt, R. (2014) Accounting for geographical variation in species–area relationships improves the prediction of plant species richness at the global scale. *Journal of Biogeography*, 41, 261–273.

Journal of Biogeography (J. Biogeogr.) (2014) 41, 261–273

Journal of Biogeography

ORIGINAL ARTICLE

Accounting for geographical variation in species–area relationships improves the prediction of plant species richness at the global scale

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ABSTRACT

Aim The species–area relationship (SAR) is a prominent concept for predicting species richness and biodiversity loss. A key step in defining SARs is to accurately estimate the slope of the relationship, but researchers typically apply only one global (canonical) slope. We hypothesized that this approach is overly simplistic and investigated how geographically varying determinants of SARs affect species richness estimates of vascular plants at the global scale.

Location Global.

Methods We used global species richness data for vascular plants from 1032 geographical units varying in size and shape. As possible determinants of geographical variation in SARs we chose floristic kingdoms and biomes as biogeographical provinces, and land cover as a surrogate for habitat diversity. Using simultaneous autoregressive models we fitted SARs to each set of determinants, compared their ability to predict the observed data and large-scale species richness patterns, and determined the extent to which varying SARs differed from the global relationship.

Results Incorporating variation into SARs improved predictions of global species richness patterns. The best model, which accounts for variation due to biomes, explained 46.1% of the species richness variation. Moreover, fitting SARs to biomes produced better results than fitting them to floristic kingdoms, supporting the hypothesis that energy availability complements evolutionary history in generating species richness patterns. Land cover proved to be less important than biomes, explaining only 36.4% of the variation, possibly owing to the high uncertainty in the data set. The incorporation of second-order interactions of area, land cover and biomes did not improve the predictive ability of the models.

Main conclusions Our study contributes to a deeper understanding of SARs and improves the applicability of SARs through regionalization. Future models should explicitly consider geographically varying determinants of SARs in order to improve our assessment of the impact of global change scenarios on species richness patterns.

Keywords
Biodiversity, biome, conservation biogeography, floristic kingdom, land cover, power law, simultaneous autoregressive model, vascular plants.

INTRODUCTION

The species–area relationship (SAR) is one of the most intensely studied patterns in ecology and has profound importance for conservation biogeography (Ladle & Whittaker, 2011). Applications of this concept range from mapping global species richness patterns (Kier *et al.*, 2005) and estimating future extinction rates (Thomas *et al.*, 2004; Sala *et al.*, 2006; van Vuuren *et al.*, 2006) to supporting conservation decision-making (Ladle & Whittaker, 2011). The theory underlying

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SARs is fundamental to both our understanding of biodiversity and our ability to conserve it (Turner & Tjørve, 2005; Drakare *et al.*, 2006; Dengler, 2009), yet questions of how various factors at the global scale influence the parameterization of SARs are not completely understood (Turner & Tjørve, 2005; Whittaker & Fernández-Palacios, 2007).

The most prominent way to relate species richness (S) to sampling area (A) is to apply the power law model (Arrhenius, 1921), because it has been shown to describe SARs appropriately under most conditions (Connor & McCoy, 1979; Dengler, 2009; Triantis *et al.*, 2012). The equation takes the form of:

$$S = c \times A^z \tag{1}$$

or its linear function in the log–log space:

$$\log(S) = \log(c) + z \log(A). \tag{2}$$

The intercept c can be interpreted as the average number of species per unit area (e.g. $A = 1$), and z describes the slope of the log–log relationship. Regardless of which mathematical model is used to construct the SAR curve, accurate estimation of the slope is a key step in defining the relationship. Although a wide range of z-values has been reported (e.g. Drakare *et al.*, 2006), a restricted range of values has been used for extinction estimates, typically ranging from $z = 0.15$ to $z = 0.25$ or 0.35 (e.g. Pimm *et al.*, 1995; Brooks *et al.*, 2002; Thomas *et al.*, 2004). The use of these restricted values is based on several theoretical assumptions (Preston, 1962; Harte & Kitzes, 2012), but is not empirically validated. In fact, the z-values of SARs strongly depend on the processes establishing species richness and composition patterns, and thus should reflect the spatial and temporal scale of the studied system (Rosenzweig, 1995; Turner & Tjørve, 2005).

Three determinants might explain the slope for species richness versus area (Rosenzweig, 1995; Turner & Tjørve, 2005). First, larger areas harbour more individuals, leading to more species being recorded (sampling artefact); second, larger areas cover more types of habitat and land cover (habitat diversity); and finally, larger areas contain more biogeographical provinces (evolutionary independence). However, factors determining SARs might differ among spatial scales (Shmida & Wilson, 1985; Rosenzweig, 1995; Turner & Tjørve, 2005; Triantis *et al.*, 2012). While the sampling artefact is relevant at small spatial scales (10^0–10^4 m²), Turner & Tjørve (2005) suggest that habitat diversity influences species richness at all spatial scales (up to 10^8 km²) and biogeographical provinces at large scales (10^4–10^8 km²).

At the macroscale, not only area but also evolutionary history and ecosystem productivity are the most important correlates of species richness patterns (Blackburn & Gaston, 2003; Storch *et al.*, 2007; Kisel *et al.*, 2011). Because area is already captured in SAR models we need to account for its interactions with history and productivity. Specifically, history and productivity drive differences in diversification rates, i.e. the rates at which speciation, immigration and extinction operate, now and in the past (Rosenzweig, 1995; and see Storch *et al.*, 2007; for review). For rates of speciation and extinction two general explanations are commonly suggested (Mittelbach *et al.*, 2007; Kisel *et al.*, 2011): time for speciation and net rate of diversification. For instance, historical processes such as plate tectonics, glaciation and climate change set the scene for speciation processes (Blackburn & Gaston, 2003). Furthermore, higher productivity may lead to higher speciation rates and/or lower extinction rates, and thus to the latitudinal decline of species richness (Mittelbach *et al.*, 2007; Storch *et al.*, 2007). In the more recent past and at a smaller scale, humans started to transform land and, hence, established new environmental conditions and habitats promoting extinction and immigration of non-native species. Thus land use might also influence SARs.

Several studies have attempted to incorporate variation into SAR models at the global scale using surrogates for the mechanisms behind species richness variation (Rosenzweig, 1995; Kier *et al.*, 2005; van Vuuren *et al.*, 2006). Their results suggest that biogeographical units, in particular biomes or floristic kingdoms, are likely to influence SAR parameterization for vascular plants. However, a quantitative comparison with a global SAR regarding predictive accuracy is needed. Floristic kingdoms represent regions of similar evolutionary history. They share a similar history of isolation and evolution (because of climate change and catastrophes) that may have caused differences in diversification rates and, hence, variation in SARs. Biomes are generally defined as major types of natural vegetation originating from a particular mix of climatic and edaphic conditions (Olson & Dinerstein, 1998; Ladle & Whittaker, 2011). Because biomes vary widely in per-area measurements of plant biomass and net primary productivity (Millennium Ecosystem Assessment, 2005), they may serve as a surrogate for ecosystem productivity. Further, evolutionary history and ecosystem productivity influence SARs for vertebrate taxa (Hurlbert & Jetz, 2010; Kisel *et al.*, 2011). However, biomes also have an origin in time and their characteristics depend on both ecological and phylogenetic constraints (Pennington *et al.*, 2004). On that account, the hypotheses of evolutionary history and ecosystem productivity as determinants of differing SARs are not mutually exclusive (Qian & Ricklefs, 2004).

Previous studies that account for geographical variation of habitat or land cover in SARs have typically focused on relatively limited spatial extents. For example, the meta-analysis of Drakare *et al.* (2006) and the review by Watling & Donnelly (2006) reveal that SAR slopes strongly reflect the latitudinal gradient of species diversity and greatly differ among different habitats and matrix types. These syntheses of small-scale studies underpin the hypothesis that spatial variation of habitat diversity and land cover affects SARs, but our understanding of how these determinants influence the estimation of SARs at the global scale is limited. Land cover is determined by the physical and biological cover of the land surface, which in turn depends on climate, topography and soil, and partly on human land use. Thus, land cover is closely related to biome classification and serves as a proxy for land use, which may be primarily responsible for global biodiversity loss (Sala *et al.*, 2000). Previous studies aiming to estimate future species loss consider the effects of land cover only in the form of habitat loss caused by agricultural expansion, thereby assuming zero species after conversion (Sala *et al.*, 2006; van Vuuren *et al.*, 2006). However, landscape transformation does not imply that habitat becomes completely inhospitable, but rather that there will be taxon-specific changes in the slope of SARs (Koh & Ghazoul, 2010).

The aim of this study was to identify the importance of different drivers in determining SARs of vascular plants at large scales (10^1 to 6×10^5 km²). Using species richness data of vascular plants in 1032 geographical units differing in size and shape (Kreft & Jetz, 2007), we examined the effects of floristic kingdoms, biomes and land cover as determinants of SAR variation. In contrast to other studies that consider habitat heterogeneity by accounting for the number of different habitats (the choros model; Triantis *et al.*, 2003), we adopted a novel approach of fitting SARs to habitat classes separately similar but not identical to the habitat–unit model of Buckley (1982). Moreover, we considered interactions between biomes and land cover. We hypothesized that geographical regionalization of SARs considerably improves the prediction of global species richness patterns and their applicability. Specifically, both over- and underestimation of species richness would be reduced compared to a single global relationship. Furthermore, since biomes capture both evolutionary history and ecosystem productivity (Pennington *et al.*, 2004), biomes should better explain species richness than do floristic kingdoms. Finally, we tested whether incorporating land cover and human uses, which comprise small-scale properties other than ecosystem productivity (see above), leads to improved predictions, and whether land-cover effects on SARs vary between biomes.

MATERIALS AND METHODS

Species data

We used global species richness data of vascular plants derived from floras, checklists and other literature sources for 1032 geographical units representing natural or administrative units, such as countries or protected areas (Fig. 1; for details see Kier *et al.*, 2005; Kreft & Jetz, 2007). We excluded oceanic islands because isolation and geology dominate species richness patterns there (Rosenzweig, 1995; Whittaker & Fernández-Palacios, 2007; Kreft *et al.*, 2008). The sampling units in our data set differed substantially in size and shape (areas ranged between 13.5 km² and 575,440 km²). Thus, we based our analysis on type IV SAR curves, derived from independent units (cf. Scheiner, 2003). Although large gaps existed in the data (e.g. Brazilian Amazon), the data set covered almost the full spectrum of global variation in abiotic conditions.

Environmental data

In order to examine the impact of the driving factors behind species richness variation reflected in SARs, we examined four determinants. First, we chose floristic kingdoms (Good, 1974), which represent regions of similar evolutionary history in which species originate by speciation. In total, there are six floristic kingdoms (Fig. 2a). Second, we examined the species–area effect in biomes, which are characterized by similar environmental conditions and unique collections of ecosystems and species assemblages (Olson & Dinerstein, 1998). Olson & Dinerstein (1998) defined 14 biomes (Fig. 2b). However, we excluded mangroves from our analysis owing to the lack of sampling units in this biome.

Third, in order to identify the effect of different land-cover classes on SARs, we chose the HYDE 2.0 database (Goldewijk, 2001), which consists of 16 land-cover classes (Fig. 2c) and provides models of past, present and future land cover. Two of these land-cover classes describe the use of land by humans (i.e. cultivated land and pastures). However, the species richness data used in our study did not represent a snapshot of a single year but rather incorporated knowledge that was accumulated over decades or centuries. Although species data were collected from areas with minimal human involvement, humans have had an impact on the world's land cover for hundreds of years, and the human presence should not be completely disregarded. Thus, we decided to test land-cover data from three different time steps: 1700 (i.e. before the onset of industrialization and large-scale transformation of agricultural areas), 1800 and 1900. Owing to scarce species richness data in regions covered with ice, tundra and wooded tundra, we decided to exclude these classes from the analysis, resulting in a total of 13 land-cover classes.

Fourth, because of regional variation in species richness (e.g. the latitudinal gradient), we hypothesized that the effects of area per land cover class also vary among regions. We chose biomes to test for this regional variation. However, biomes and land cover are reasonably well correlated in the sense that in most biomes only a subset of land-cover classes appears. For this reason, and in order to reduce degrees of freedom, we simplified biomes and land-cover classification by aggregating similar classes. Using regression tree analysis (De'ath & Fabricius, 2000), biomes were aggregated with respect to the ratio of log(species richness) per log(area). We divided the data into four regions of aggregated biomes to ensure that each had enough data for the analysis and the HYDE 2.0 land-cover classes were reorganized into four classes: forest, grassland, cropland, ice and deserts (see Appendix S1 in Supporting Information for more details). We assigned each sampling unit to the prevailing floristic kingdom; however, we computed the percentage coverage for each biome and land-cover class per sampling unit.

Statistical analyses

We $\log_{10}$-transformed species richness and area to linearize the power-law relationship and allow the use of simple linear regressions. The power law is generally the most appropriate for describing SARs (Connor & McCoy, 1979;

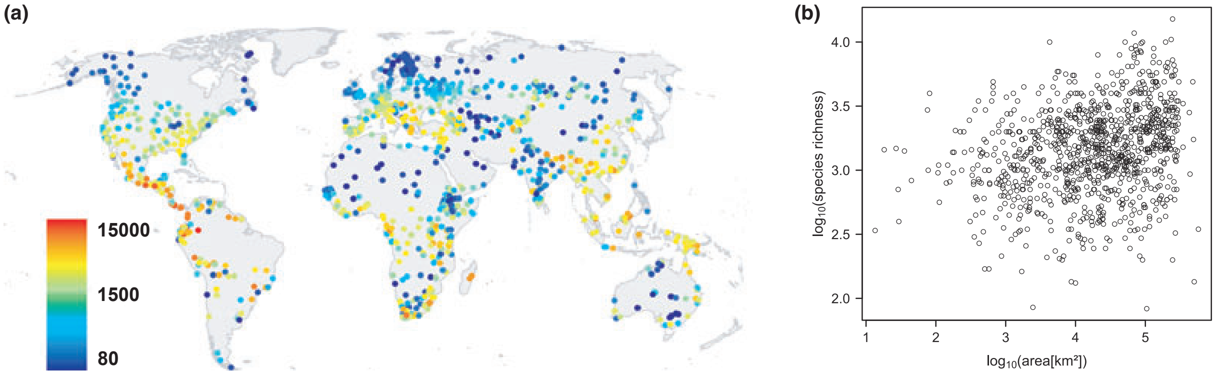

Figure 1 (a) Geographical distribution of richness data for vascular plants used in the analysis (n = 1032, after Kreft & Jetz, 2007). Dots represent centres of geographical units. Geographical units differ in size, and species counts have not been standardized; (b) observed relationship of $\log_{10}$(species richness) against $\log_{10}$(area).

Dengler, 2009; Triantis *et al.*, 2012) and its parameters are comparable among the majority of SAR studies (Dengler, 2009). In addition to the power law, we also tested the logarithmic model (Gleason, 1922). In line with the literature (Connor & McCoy, 1979; Dengler, 2009; Triantis *et al.*, 2012), this model had worse fits and is discussed only in Appendix S2.

Because spatial autocorrelation was present in the data, we employed simultaneous autoregressive models assuming spatial autocorrelation in the error term and using the R 2.15.2 statistical analysis software package (R Development Core Team, 2012), function *spautolm* in the package SPDEP (Bivand *et al.*, 2012). This method includes a second error term that explicitly models spatial dependence in the residuals (Dormann *et al.*, 2007; Bivand *et al.*, 2008) and has been shown to be a robust method to account for spatial autocorrelation (Kissling & Carl, 2008; Beale *et al.*, 2010). We defined a weighted neighbourhood structure that best modelled the spatial structure in the residuals, thus minimizing spatial autocorrelation in the independent error term (cf. Kissling & Carl, 2008). Based on minimization of the Akaike information criterion (AIC), which in our case also minimized residual spatial autocorrelation (RSA), we concluded that a neighbourhood distance of 700 km accounted best for the spatial structure in the data (Appendix S3: Fig. S3.1).

We compared nine different models. The first model fitted the species–area effect globally, and the second and third model fitted the effect into biogeographical regions separately. We considered biogeographical regions of floristic kingdoms as dummy variables while considering biomes as percentage cover of sampling units. Three models considered the species–area effect per land-cover class for the three different time steps. Analogous to biomes, all land-cover classes were calculated as percentage cover of sampling units and treated as additional predictors. We performed weighted regressions between area and region, and between area and land cover, and included first-order interactions. Finally, three models fitted the SARs to aggregated land-cover classes and aggregated biomes, again one for each of the three time steps. Here, we fitted both first-order interactions between area and region, and between area and land cover, and we fitted second-order interactions between area, regions and land-cover classes. We selected the best model for each set of variables based on the lowest AIC.

We ranked the resulting models by AIC because the number of predictors varied greatly between each model. We report ΔAIC (i.e. the difference between model AIC and the minimum AIC relating to the best model) and AIC weights (Burnham & Anderson, 2002). To account for overfitting, we compared the ability of each model to predict independent data (i.e. not used during the fitting process) via 10-fold cross-validation (see Harrell, 2001).

For the purpose of comparing the predictive ability of the various models, we plotted observed versus predicted log(species richness) and the histogram of the prediction errors [i.e. $\log_{10}(\text{pred}) - \log_{10}(\text{obs})$]. Prediction errors are similar to the residuals of the SAR model but do not account for spatial autocorrelation. Prediction errors can be interpreted as the percentage of over- or underestimation in log-space, where positive values indicate overestimation and negative values indicate underestimation of the observed richness.

To determine the extent that various SARs differ from the global relationship, we plotted the SAR curves and calculated 95% confidence intervals of the model forecast uncertainty for each SAR (Neter *et al.*, 1996), i.e. the confidence limits around the mean Y_h using the standard deviation of the forecast:

$$s^2 = \mathrm{MSE} \times \left(X_h^{\,T}(X^T X)^{-1} X_h\right), \qquad (3)$$

where MSE is the mean square error of prediction and X is the model matrix with intercept and predictor variable area. We considered differences compared to the global SAR to be significant when the corresponding 95% confidence intervals did not intersect with the 95% confidence intervals

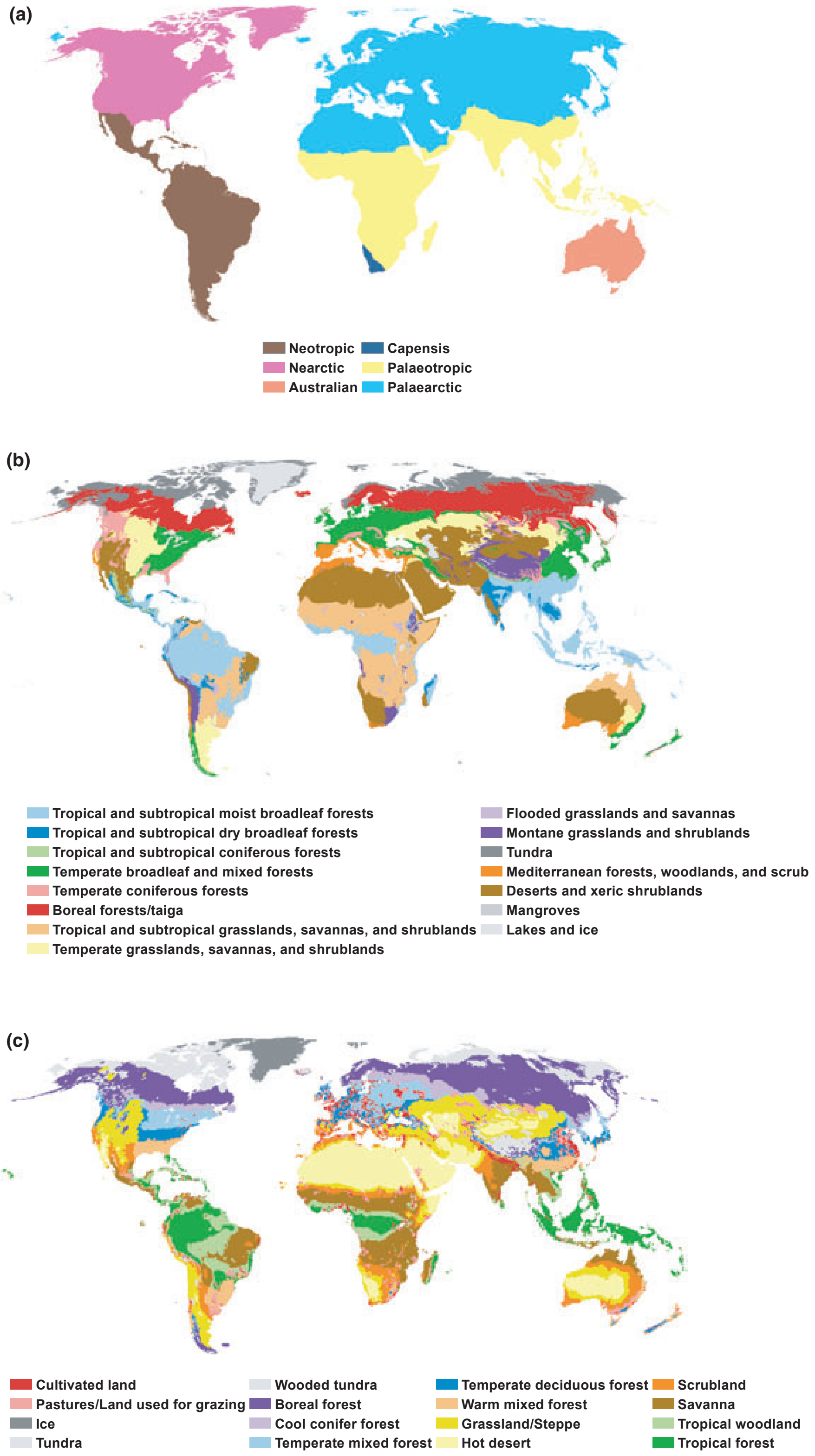

Figure 2 Maps of potential factors causing variation of species–area relationships (SARs) for vascular plants analysed in this study: (a) floristic kingdoms (following Good, 1974), (b) biomes (following Olson & Dinerstein, 1998), (c) modelled land cover of the year 1700 (based on data from the HYDE 2.0 database; Goldewijk, 2001). The maps are projected using the Robinson projection.

of the global model over the entire range of the sampling area.

Owing to our spatially explicit modelling approach, parameter estimates depended on the spatial arrangement of the fitted data. In order to quantify the impact of spatial configuration of samples on parameter estimates, we repeated the fitting process 1000 times using bootstrap resampling from the original data. Finally, we compared the means and standard errors of parameter estimates using the entire data set and the bootstrap samples to fit model parameters.

In addition to an overall improvement of different SARs compared to the global SAR (explained as AIC and R^2), we investigated model performance in a spatially explicit manner. First, we applied different SAR models to predict the species richness pattern based on a 100 km × 100 km grid. Second, we calculated and plotted the prediction errors based on the raw data points.

RESULTS

During model selection, none of the biogeographical regions, floristic kingdoms and biomes was excluded. This consideration means that separately fitting the SAR parameters for each region improved model performance, i.e. exclusion of a particular effect would have led to a higher AIC. First-order interactions with area in the land-cover model (LC) were selected for the land-cover classes cultivated land, boreal and cool conifer forest, warm mixed forest, scrubland, savanna and tropical forest. The model that fitted the area effect to aggregated land-cover classes and biomes (LCcombstrat) included all variables (interactions between regions and the land-cover class ‘ice and desert’ were not modelled).

Table 1 Species–area relationship (SAR) models for vascular plants compared by degrees of freedom, ΔAIC values with respect to the best model, AIC weights and mean predictive ability R^2 computed by 10-fold cross-validation. Variation of SARs improves prediction of the species richness pattern. Model names refer to determinants used to account for variation in SARs: global SAR, varying SARs by floristic kingdoms, biomes, land cover for baseline years 1700, 1800 and 1900, and combined land-cover classes and aggregated biomes for baseline years 1700, 1800 and 1900.

Model	d.f.	ΔAIC	AIC weights	R^2
Global	1	220.41	0.000	0.059
Floristic Kingdoms	11	184.87	0.000	0.162
Biomes	25	0.00	1.000	0.461
LC1700	20	36.72	0.000	0.364
LC1800	19	48.40	0.000	0.348
LC1900	16	50.49	0.000	0.346
LC1700combstrat	30	32.23	0.000	0.377
LC1800combstrat	30	33.91	0.000	0.371
LC1900combstrat	30	43.14	0.000	0.372

AIC, Akaike information criterion.

Apart from model improvement indicated by lower AIC values, we found evidence that models with data separately fitted to each biogeographical region considerably improved the explanation of species richness patterns (R^2, Table 1). The global SAR explained only 6% of the variability in species richness; however, SARs based on biomes explained 46.1%. Hence, SARs fitted to biomes performed better than those fitted to floristic kingdoms (16.2%) or land cover (36.4%). However, combining biomes and land cover in second-order interactions did not considerably outperform models with only first-order interactions. Because models built using land cover for the year 1700 or biomes as predictors produced the best results, we limited the following report to their investigation.

We found that SARs differ in their intercept and slope (Fig. 3, Table 2). Thus, modelling according to one global relationship would lead to over- or underestimation of species richness, depending on the compositional characterizations of the area of interest. In the biome model, intercepts of the SARs ranged between 19.4 species per km^2 in the flooded grasslands and savannas biome and 364.8 species per km^2 in the boreal forests/taiga biome. Note that these intercepts resulted from extrapolation beyond the ranges of polygon area in our species data (Fig. 3a). The boreal forest/taiga biome also had the lowest slope estimate (0.078), which indicates little effect of area. The maximum slope of 0.454 was found in the tropical and subtropical coniferous forests biome.

Land-cover specific SARs also displayed a large range in their parameters (Fig. 3, Table 2). The intercepts in the LC model ranged from 64.7 species per km^2 for deserts to 578.1 species per km^2 for cool conifer forests, which also have the shallowest slope (0.065). For some land-cover classes, we did not find significant interactions with area, and the area effect was reduced to 0.177 to match the global slope of the LC model.

Within the range of polygon area, biomes of deserts, tundra and boreal forest/taiga contained fewer species, while tropical, mediterranean and temperate forest biomes contained far more species than estimated by the global SAR (Fig. 3). Land-cover classes in the LC model behaved similarly to the corresponding biomes: the desert contained the lowest number of species, and the tropical forest contained the highest number of species.

The specific differences in the biome- and land-cover SAR curves versus the global SAR curve were significant within the given area range in all cases except for the biome tropical and subtropical dry broadleaf forests (Appendix S3: Fig. S3.3). Outside a particular area range, species richness estimates from the global SAR became worse. Furthermore, most SAR curves showed significant differences from the global SAR curve over the entire area range. Thus, the application of a global SAR for these biomes and land-cover classes resulted in consistent and partly substantial over- or underestimation across the entire area range.

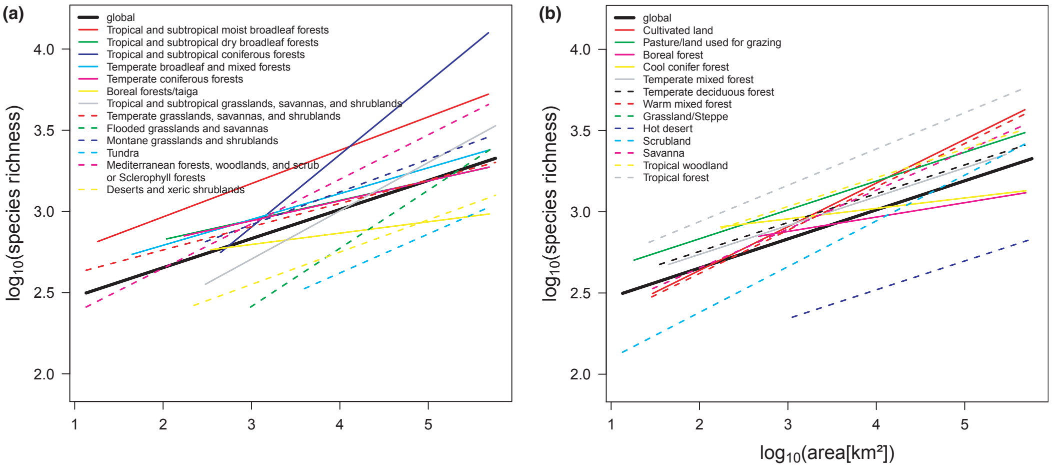

Figure 3 Differences in species–area relationship (SAR) curves for vascular plants among (a) biomes and (b) land-cover classes. Axes delineate ranges of original data (see Fig. 1b). The thick black line indicates the global relationship. The lengths of SAR curves reflect the range sizes of sampling units used to fit the relationship. Note that the SAR curve for land-cover grassland/steppe is not visible because it differs only marginally from the global SAR.

Table 2 Differences in species–area relationship (SAR) parameters for vascular plants for three models: the intercept $\log_{10}(c)$ and slope z of SARs in log–log space (parameters refer to equations (1) and (2)), and the number of samples (n) used to fit effects of predictors, i.e. the number of sampling units that contain a particular biome or land-cover class. Equal parameter values imply the exclusion of interactions during model selection. The remaining columns provide information about the species richness estimates per 10,000 km² and the range sizes of sampling units used to fit the relationship. Area of sampling units was measured in km².

	n	$\log_{10}(c)$	z	Species richness per 10,000 km²	min(range)	max(range)
Global model						
Global	1032	2.296	0.179	1028.016	13.5	575439.9
Biome model						
Tropical and subtropical moist broadleaf forests	121	2.522	0.212	2344.229	18.2	301995.2
Tropical and subtropical dry broadleaf forests	140	2.562	0.126	1164.126	1349.0	346736.9
Tropical and subtropical coniferous forests	36	1.537	0.454	2254.239	13.5	575439.9
Temperate broadleaf and mixed forests	24	2.468	0.161	1294.196	1096.5	141253.8
Temperate coniferous forests	313	2.562	0.127	1174.898	26.9	478630.1
Boreal forests/taiga	398	2.562	0.078	748.170	112.2	501187.2
Tropical and subtropical grasslands, savannas, and shrublands	1032	1.765	0.310	1011.579	13.5	575439.9
Temperate grasslands, savannas, and shrublands	1032	2.475	0.144	1124.605	13.5	575439.9
Flooded grasslands and savannas	1032	1.287	0.370	584.790	13.5	575439.9
Montane grasslands and shrublands	1032	2.260	0.215	1318.257	13.5	575439.9
Tundra	1032	1.634	0.250	430.527	13.5	575439.9
Mediterranean forests, woodlands, and scrub or sclerophyll forests	1032	2.080	0.280	1584.893	13.5	575439.9
Deserts and xeric shrublands	1032	1.926	0.205	557.186	13.5	575439.9
Land-cover model						
Cultivated land	323	2.102	0.269	1506.607	29.5	478630.1
Pasture/land used for grazing	412	2.480	0.177	1541.700	18.2	478630.1
Boreal forest	186	2.612	0.089	928.966	467.7	489778.8
Cool conifer forest	144	2.762	0.065	1051.962	173.8	489778.8
Temperate mixed forest	231	2.384	0.177	1235.947	44.7	295120.9
Temperate deciduous forest	227	2.402	0.177	1288.250	35.5	478630.1
Warm mixed forest	192	2.087	0.267	1428.894	28.8	478630.1
Grassland/Steppe	258	2.219	0.177	845.279	13.5	575439.9
Hot desert	119	1.811	0.177	330.370	1122.0	575439.9
Scrubland	234	1.816	0.282	879.023	13.5	501187.2
Savanna	222	2.176	0.239	1355.189	29.5	478630.1
Tropical woodland	152	2.501	0.177	1618.080	177.8	478630.1
Tropical forest	154	2.495	0.223	2437.811	26.9	426579.5

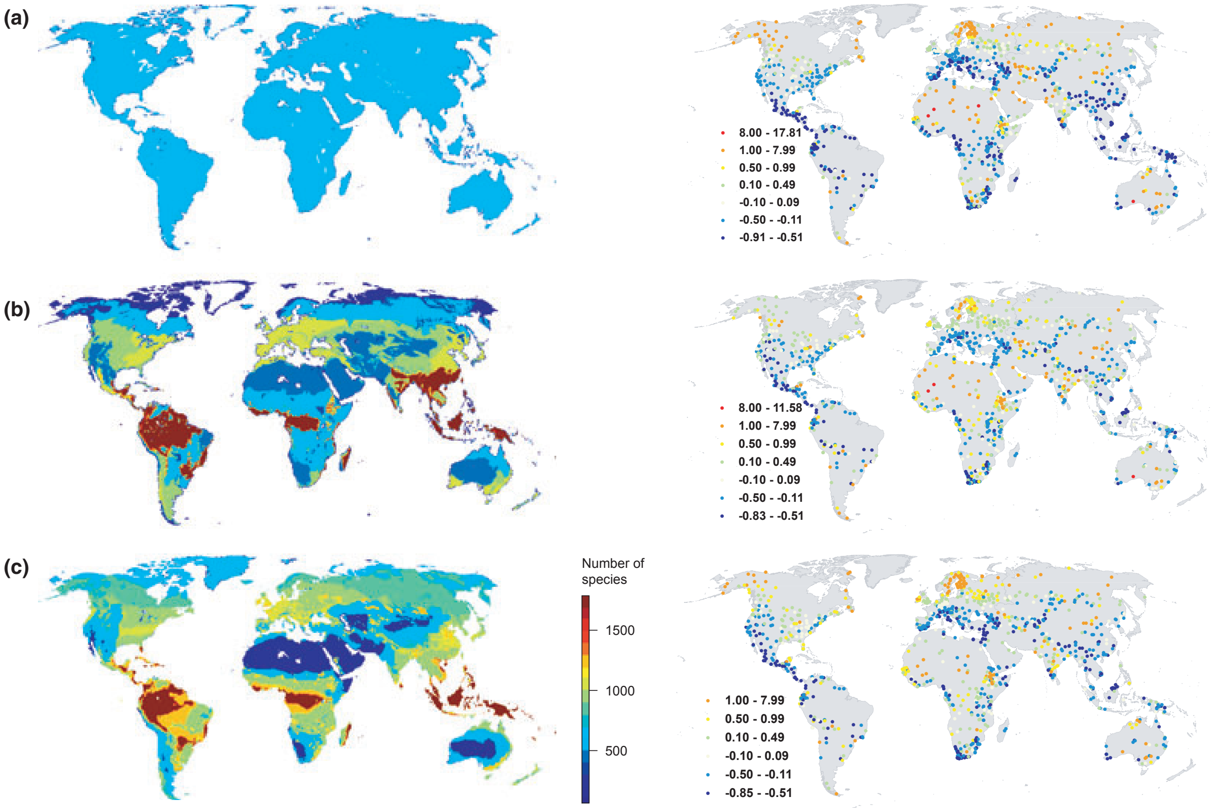

Figure 4 Left column: Predictions of vascular plant species richness for 100 km × 100 km grid cells based on (a) a global species–area relationship (SAR), or varying SARs by (b) biomes or (c) land cover. Right column: The prediction error ($\log_{10}(\text{pred})-\log_{10}(\text{obs})$) for the corresponding models based on data points from raw data: red for underestimations, blue for overestimations, and green for all the predictions close to reality (i.e. between -0.2 and $+0.2$). The maps are projected using the Robinson projection.

After fitting 1000 bootstrap resamples, we found that spatial dependence was of marginal importance for parameter estimates. We compared parameter estimates from the entire data set with those of the bootstrap resamples and found that the means of each parameter estimate were nearly equal across all samples regardless of spatial configuration, i.e. the estimates were unbiased and there was no systematic over- or underestimation. However, confidence intervals of the error estimates were narrower when the entire data set was used (Appendix S3: Fig. S3.4).

Varying SARs with biomes or land cover improved predictions of species richness patterns relative to the global SAR model. Accordingly, world maps of species density at 100 km × 100 km showed considerably different patterns (Fig. 4). The global SAR predicted a constant species density for all cells except coastlines. This result was an artefact of the data resolution because coastline areas only partially overlapped the 100 km × 100 km cells. Biome and land-cover SARs identified a well-known macroecological pattern, i.e. the latitudinal gradient (e.g. Ladle & Whittaker, 2011). In addition, the LC model predicted variation of species richness also at smaller scales. However, we lacked data to test the accuracy of the models at finer scales.

Predicting the raw data, both the biome and the LC model produced smaller prediction errors (maximum 1.12 and minimum -0.83, i.e. maximal overestimation of 112% and underestimation of 83% of observed richness on the log-scale) and a narrower distribution around zero compared to the global model (Fig. 4 right column, Fig. 5). Colours in Fig. 4 right column show localities where improvements were achieved. Notably, there were three polygons for which the biome model highly overpredicted the actual species richness (Fig. 5b, prediction errors of 1.035 to 1.12). These polygons contained a considerable amount of desert. Apart from these outliers, the biome model improved predictions across the entire area (prediction errors ranged from -0.765 to 0.754).

DISCUSSION

We found evidence that the relationship between species richness and sampled area differs considerably across the globe. The use of geographically varying SARs not only improves predictions of species richness but our modelling approach also allows easy implementation in applied studies. The number of species in a given area *A* can be estimated by summing up species richness estimates for

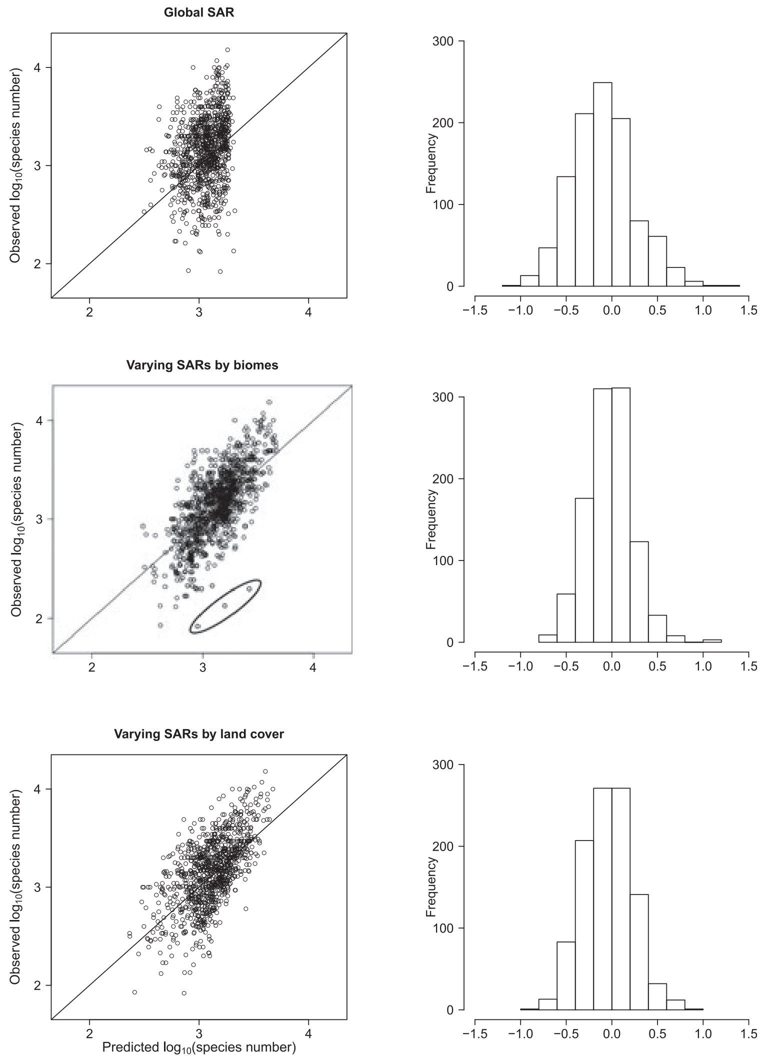

Figure 5 Quantitative analysis of model improvement for species–area predictions for vascular plant richness. Left column: observed versus predicted richness plot. Outliers in the biome model, to which we referred in the text, are highlighted by the ellipse. Right column: histogram of absolute prediction errors.

each class of determinants (e.g. floristic kingdoms, biomes, land cover):

$$\log_{10}S = \sum_i (\log_{10}c_i + z_i \log_{10}A) \times \%\, R_i \qquad (4)$$

where i denotes the classes (i.e. c_i, z_i are SAR parameters), $\%R_i$ is the percentage area covered by the corresponding class (e.g. biomes), and $\sum_i \%R_i = 1$.

Determinants of geographical variation in SARs

We showed that several geographically varying factors help to explain SARs. First, the total number of species in a study area depends on its location in addition to its area. Thus, a small sampling unit in one biome, floristic kingdom or land-cover type can have more species than a larger unit in a different biome, floristic kingdom or land-cover type (Fig. 3). These differences are caused by regional variation in species density, as reflected in the various intercepts, and by the increase in species richness per unit area, as reflected in differing slopes. For instance, the global model almost always overestimates species richness in particularly species-poor regions such as the tundra biome, whereas it underestimates species richness in the biome of tropical and subtropical moist broadleaf forests (Fig. 3a). Whether species richness in other biomes such as tropical grasslands, savannas and shrublands is over- or underestimated depends on the size of the area of interest.

Second, depending on the location of interest, the global model under- or overestimates species richness, while region-specific SARs provide more accurate results. Regarding optimal regionalization, we conclude that for SAR parameterization regions are better distinguished by biomes than by floristic kingdoms because biomes explained more of the variation in species richness (46% compared with 16%, cf. Table 1). Thus, the results suggest that ecosystem productivity and evolutionary history, both captured in biomes, determine the patterns of plant species richness. Future studies using better predictors and possibly more specific hypotheses can use this proposed approach to test the role of specific processes in generating observed richness patterns.

Third, land cover is a less important factor in species richness variation than biomes (Table 1). Hence, land-use features, in addition to ecosystem productivity, do not improve the ability of models to explain the variation in species richness. Comparing the different time steps, we conclude that the SAR model works best for the year 1700. This result supports the suggestion made by Kier *et al.* (2005) that the data reflect native species richness rather than the current situation including introduced species and recent species extinction. Moreover, as land cover included additional small-scale properties such as human land uses (even though the data used are still relatively coarse, at 100 km × 100 km), the LC model predicted a wider range of species richness (Figs 4 & 5). However, we were not able to independently confirm these predictions because of the lack of raw data for equal area grids.

Although we found that the independent use of biomes and land cover improved SARs considerably, the models created using both the aggregated land-cover and biome classes did not bring additional improvements (Table 1, LCcombstrat 1700–1900). As the number of data points did not permit a factorial combination of biogeographical regions and land-cover classes, our combinations may have been suboptimal. However, an alternative aggregation of land-cover classes produced less accurate results (data not shown).

Overall, accounting for regional variation in SARs substantially improved the predictive ability of our models (Fig. 4 right column). However, using a regional area defined by biomes or land cover still did not detect the entire range of species richness. We show that models mostly overestimate species richness in higher latitudes and deserts but underestimate species richness in biodiversity hotspots (*sensu* Myers *et al.*, 2000) such as south Central China, Cape Floristic Province, Succulent Karoo, Mesoamerica, western Ecuador and the Mediterranean Basin. The underestimation could be due to other factors that more directly influence the degree of species diversity, such as climatic constraints at smaller scales, which do not appear in biome or land-cover classification.

The diversity of human-dominated land

Contrary to our expectation, land-cover SAR curves (Fig. 3) indicate that human transformed landscapes, such as cultivated land and grazed pastures, contain a large number of plant species and show a relatively high increase in species richness per area compared with SARs of natural vegetation. In fact, several studies suggest that areas suitable for humans coincide with areas that are suitable for maintaining a large number of species (Araújo, 2003; Kühn *et al.*, 2004). In some cases, the introduction of human-dominated habitat can also cause an increase in the species density (e.g. Araújo, 2003; Desrochers *et al.*, 2011), especially in areas with a long history of human settlement (e.g. Europe, parts of China and India). For example, non-native plants are often introduced by human inhabitants of agricultural regions, and thus increase the species richness variation. Additionally, smaller losses of natural habitat (up to a certain threshold) might increase species richness because of increased habitat heterogeneity in otherwise homogeneous natural areas, and thus increase available habitat for open-habitat species (Desrochers *et al.*, 2011). However, we need to be cautious with the interpretation of the SAR curve for cultivated land. As Desrochers *et al.* (2011) point out, progressive conversion of natural vegetation, above a critical threshold, can lead to pronounced and rapid species loss. Thus, cultivated land potentially increases species richness only in a mix with natural vegetation, whereas in monoculture it leads to a drastic decrease.

Uncertainty and scale dependence

In addition to evaluating predictive accuracy of our models, we identified two major sources of uncertainty. The first is related to the Linnaean shortfall: species richness data come from historical sources and may be either incomplete or fail to reflect current knowledge (Ladle & Whittaker, 2011). The second source of uncertainty concerns the HYDE 2.0 land-cover data set, which estimates past distributions of main land-cover classes based on past population densities, FAO statistics, and several assumptions for cropland and pasture allocation (Goldewijk, 2001). Compared with other modelling approaches, the HYDE database predicts a later start and slower development of anthropogenic land use (Gaillard *et al.*, 2010).

Another issue is the nature of the geographical units used to compile species–area data and the distribution of samples. The geographical units used in our study represent a mixture of units delineated by vegetation and geopolitical units. For example, samples of units delineated by vegetation (e.g. protected areas) might have been less diverse in habitats because they were a priori restricted to a set of habitats. Biological interactions with adjacent areas may be reduced due to the surrounding matrix (Turner & Tjørve, 2005). In contrast, administrative units (e.g. countries) are likely to finely partition large biotically homogeneous regions in the temperate zone while agglomerating smaller biotically heterogeneous regions in the tropical zone (cf. Kisel *et al.*, 2011). As we account for the percentages of biomes and land cover, we do not expect the heterogeneous origin of our units to bias the results. Regarding the distribution of our samples, the Amazon Basin is completely missing, while Europe is over-represented. The lack of data in the Amazon Basin might affect the results for SARs of the (sub)tropical moist broadleaf forest biome and the tropical forest land cover. We expect that having more data for the Amazon Basin would result in higher *c*- and/or higher *z*-values. However, the over-representativeness of Europe should have an effect only on the model uncertainty: we expect the 95% confidence interval to be narrower due to more data.

As the determinants of SARs vary with scale (Rosenzweig, 1995; Turner & Tjørve, 2005), we strongly recommend against extrapolating our results, particularly to smaller scales. Obviously, species richness extrapolated to 1 km² is in some cases an order of magnitude or more off reality. For instance, richness estimates for the flooded grasslands and savannas biome are far too low (cf. Schmiedel *et al.*, 2010); those of the boreal forest/taiga biome far too high. Hence, our results indicate that in boreal forest/taiga biome the *z*-values below the fitted range must become steeper and in the flooded grasslands and savannas biome they must become flatter. Therefore, the *c*-values, while being the parameters of the best fitting function, have no ecological meaning. Although the reason for scale-dependency of *z*-values remains unclear (Crawley & Harral, 2001; Wilson *et al.*, 2012), population dynamics (e.g. birth, death, dispersal rates of individuals and interactions with other populations) could create spatial patterns of species richness (Crawley & Harral, 2001).

The fact that different biome- and land-cover-specific SARs intersect further illustrates the strong scale-dependency of species richness patterns. This has important implications for ranking of areas in conservation prioritization. For instance, the world records for highest species richness of vascular plants at the scale of 50 m² or less are reported from grassland systems, while at coarser spatial grains tropical lowland rain forests are clearly more diverse (Wilson *et al.*, 2012).

Expanding the models

Our models can be further expanded by evaluating the contribution of other variables related to environmental heterogeneity within sampling units. This proposal is also applicable for predicting species loss due to global change using SAR models. For instance, Koh & Ghazoul (2010) highlight the importance of considering the effects of landscape matrix when estimating species loss based on SARs. They argue that landscape transformation does not imply that a habitat becomes completely inhospitable but rather changes the number of species supported in a taxon-specific fashion. So far, these improved models have only been applied to selected taxa and small regions. With this study, by including habitat composition expressed as a percentage of biomes or land cover, we take a first step towards a matrix-calibrated SAR model for vascular plants. Developing these models further would enable us to quantify the impact and trade-offs of land-use effects on biodiversity between different plausible land-use scenarios.

CONCLUSIONS

Our study contributes to a deeper understanding of species–area relationships and global patterns of species richness. Moreover, it improves the applicability of SARs through geographical regionalization. This is particularly important for the application of SARs in conservation biogeography. Within this discipline, global analyses are becoming increasingly important, in order to assess the effects of the large-scale environmental transformation on species richness patterns.

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SUPPORTING INFORMATION

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

Appendix S1 Combinations of biomes and land-cover classes.

Appendix S2 Performance of the logarithmic model.

Appendix S3 Model selection, forecast uncertainty and spatial dependency of parameter estimates.

BIOSKETCH

Katharina Gerstner is a PhD candidate at the Helmholtz Centre of Environmental Research (UFZ) Leipzig. She is interested in investigating effects of land use on global biodiversity of plants.

Author contributions: K.G., C.D., H.K. and R.S. conceived and designed the project; H.K. gathered the data; K.G. and C.D. analysed the data; and K.G. and T.V. wrote the paper.

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

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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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*Correspondence author. E-mail: katharina.gerstner@ufz.de 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.

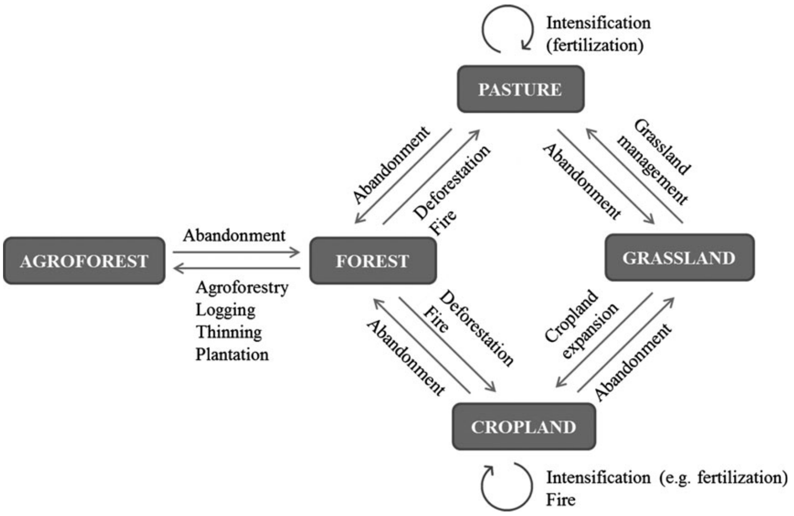

Fig. 1. Typical transitions between land-cover states and intensification (figure inspired by Lambin & Geist 2006).

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 succession) 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:

$$z = 0{\cdot}5 \cdot \ln((1+r)/(1-r)),\ \mathrm{var}(z) = 1/(n-3), \qquad \text{eqn 1}$$

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

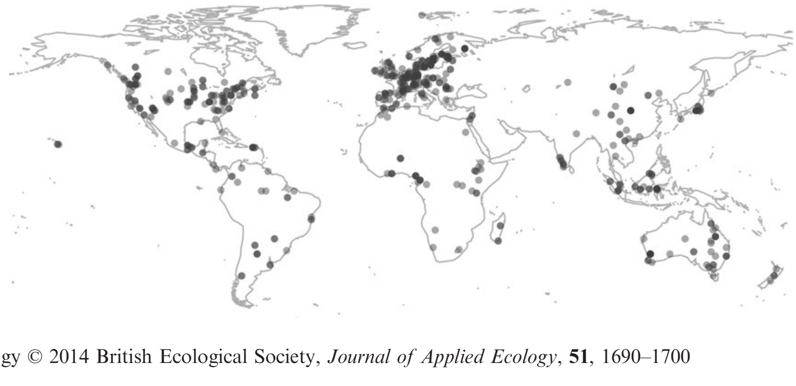

Fig. 2. World map showing the distribution of study sites. There is evidence for bias towards Europe and North America where 40·3% and 28% of studies were conducted. The majority of countries (73·5%) are not represented in the data base.

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:

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

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

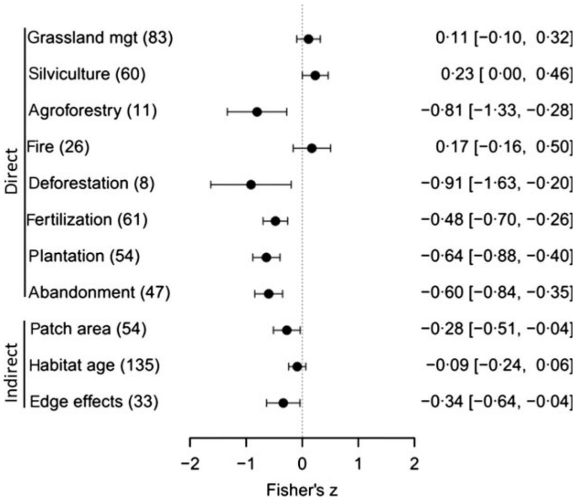

Fig. 3. Effect-size plot from the linear mixed-effects model considering land-use classes as fixed effects. Sequence according to our hypotheses stated in the introduction. Dots and bars represent mean effect sizes and their 95% CI as estimated from the model. Effect sizes indicate the direction and 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.

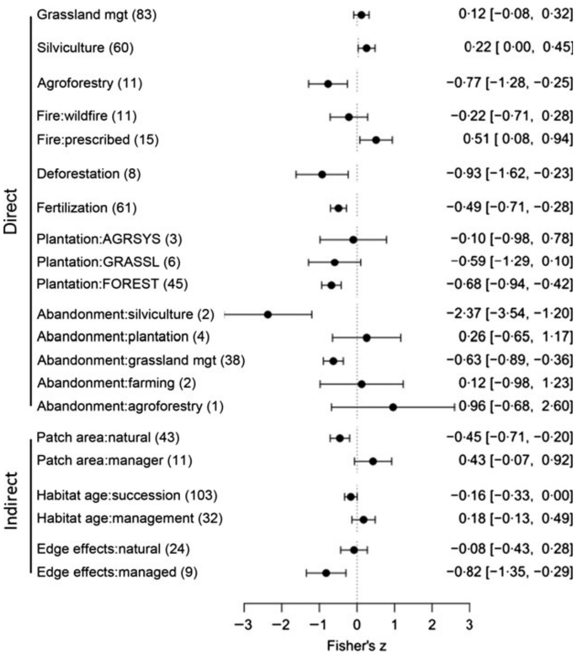

Fig. 4. Effect-size plot from linear mixed-effects models considering land-use-specific covariables, that is, wildfire vs. prescribed fire, initial land-use system for plantations, abandonment of different management classes, patch area of natural vs. managed patches, habitat age of managed vs. abandoned 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.

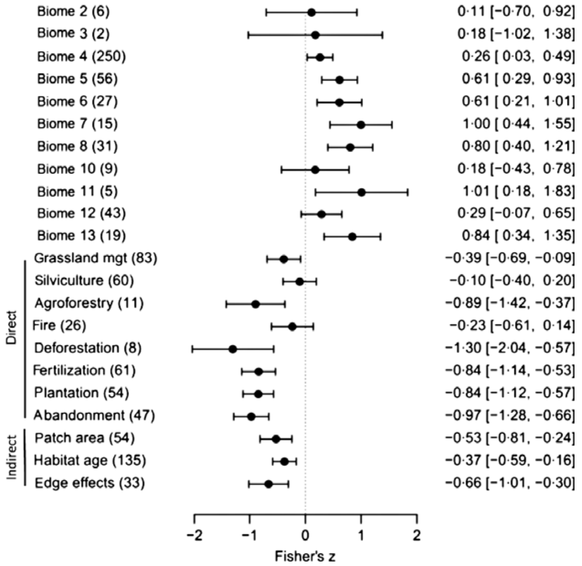

Fig. 5. Effect-size plot from the linear mixed-effects model considering additive effects of land use and biomes. Dots and bars represent mean effect sizes (Fisher's *z*) and their 95% CI as estimated from the model. Number of study outcomes is given in brackets. For interpretation of effect sizes, see 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, $r = -0{\cdot}771$, $P < 0{\cdot}005$).

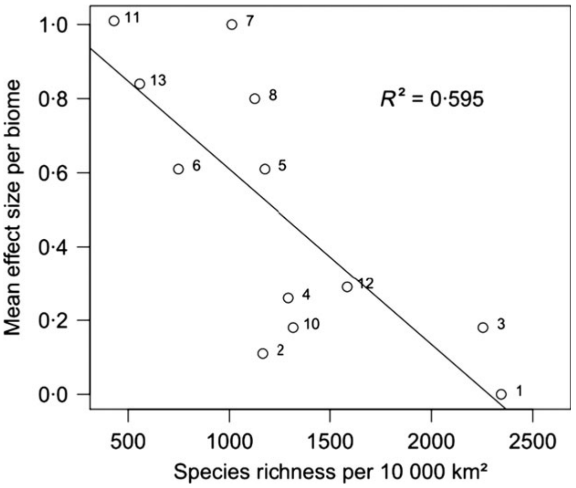

Fig. 6. Relationship between species pool size (i.e. estimated species richness per 10,000 km² *sensu* Gerstner *et al.* 2014) and mean effect size per biome. Numbers refer to biome numbers in Fig. 5 and Fig. S1 in Appendix S3 (Supporting information). Species pool size is negatively correlated with mean land-use effects per biome ($r = -0{\cdot}771$, $P < 0{\cdot}005$).

Publication bias

Using Egger's regression, we found no evidence for publication bias, neither in the land-use-only model (intercept = 0·238, $P = 0{\cdot}223$) nor in the land-use-by-covariables model (intercept = 0·250, $P = 0{\cdot}206$), or land use + biome model (intercept = 0·160, $P = 0{\cdot}432$; 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 m^2 to 1000 km^2, 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 socio-economic 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.

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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.

3.3 Integrating land use into broad-scale species richness pattern using a countryside SAR approach

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Gerstner, K., Levers, C., Kuemmerle, T., Pereira, H.M. & Seppelt, R.: Modelling land-use effects on European plant diversity using a countryside–SAR approach

Modelling land-use effects on European plant diversity using a countryside SAR approach

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ABSTRACT

Land use is considered a major threat to global biodiversity and thus need to be considered in models of biodiversity change. Especially at regional scales, where usually decisions about external factors and the allocation of conservation funds are made, improved predictions about how biodiversity is changing with changes in land use are particularly needed. Species-area models (SARs) are widely used to assess and predict biodiversity changes, but are often based on the simplistic assumption that land use leads to complete habitat loss, leaving only islands of habitat in an inhospitable matrix. This approach dramatically overestimates species loss. SAR approaches that consider the conservation value of the countryside have recently become available, but they have been limited to smaller study regions. Here, we present an improved, broad-scale SAR-approach for vascular plants that considers that species may be able to survive in human-dominated landscapes dependent on land-use intensity, and make predictions about biodiversity changes at regional to continental scales. Synthesizing findings from previous studies, we illustrate how such a model can be parameterized using the example of Europe and a rich land use dataset. We validate our model using the detailed Atlas Flora Europaeae (AFE). Overall, compared with a SAR approach which ignores land use, countryside SAR predictions result in spatially more nuanced patterns according to the spatially varying distribution of land-use indicators. Our SAR approach generally predicts higher species richness than is mapped in the AFE. Despite its limitations and uncertainties, we present a very flexible approach for which we suggest clear directions to further improve.

INTRODUCTION

Land use and changes therein are considered the major threat to biodiversity worldwide as land transformation leads to destruction, degradation, and fragmentation of habitats (Vitousek 1994, Sala et al. 2000, Millenium Ecosystem Assessment 2005). Although land use affects ecosystems at local scales, the drivers influencing individuals' land-use decisions increasingly act at continental to global scales as a result of globalization, the industrialization of agriculture and forestry, and the increasing influence of transnational cooperations, NGOs, and institutions (e.g. Lambin & Meyfroidt 2011). As many land-users are influenced by these broad-scale drivers in similar ways, the collective impact of local land-use change at broader scales can be very large.

At the same time, biodiversity loss is of great concern at the regional scale, where the level of endemism is high and usually decisions about external factors and the allocation of conservation funds are made (e.g. EU CAP, NATURA2000). Hence, a broad-scale perspective is needed to improve predictions about how land use have changed and will change biodiversity across scales. At local to regional scales, however, evidence about negative effects of land use on biodiversity, esp. species richness, is mixed (Newbold et al. 2015, Gerstner et al. 2014b) since many species can survive in human-dominated landscapes. In various regions in the world, land use has even contributed to biodiversity in a historical perspective.

Europe is an excellent example for a region with a long land-use history (Ellis et al. 2013) where many species have experienced drastic range reductions due to the expansion and intensification of land use, but also where many species today depend on low-intensity land management. In Europe, historic, low-intensity land management has resulted in a rich assemblage of species adapted to the altered environment. Today, about 50% of all species in Europe depend on agricultural habitats, including a number of endemic and threatened species (Stoate et al. 2009) and most of Europe's native forests, which have been altered by management in recent centuries (Kaplan et al. 2009), are characterized by a more homogeneous tree composition, vertical stratification, and age structure compared to a natural forest (Paillet et al. 2010). From reconstruction of historical floras it has been estimated that highest plant diversity occurred around 1850 (Poschlod et al. 2005).

However, from that period onwards, high land-use pressure resulted in changes in land use which have caused and still causes a general decrease of plant diversity in Europe. These threats include (Bengtsson et al. 2000, Poschlod et al. 2005):

- agricultural intensification through fertilization,
- reduced landscape heterogeneity by enlargement of agricultural sites,
- abandonment of less productive sites,
- and intensive forest cultivation practices, e.g. planting of monocultures and exotic species in European forests.

At broader scales, land-use effects on biodiversity (simply measured as species richness) are often assessed and predicted using species-area relationships (SARs), which are based on island biogeography theory (MacArthur & Wilson 1967). An underlying assumption of the classic SAR-approach for predicting species loss due to habitat transformation is that land-use change leads to the complete loss of habitat, leaving islands of habitat in an otherwise inhospitable matrix (e.g. Van Vuuren et al. 2006). This simplistic assumption has been heavily criticised (De Camargo & Currie 2014, Pereira et al. 2012), as species richness patterns in countryside ecosystems, i.e. areas strongly influenced by humanity, are more complex (Mendenhall et al. 2014, Pereira & Daily 2006). Different approaches have been suggested to consider that species may be able to survive in the matrix surrounding habitat patches (Tjørve 2002, Triantis et al. 2003, Pereira & Daily 2006, Koh & Ghazoul

2010). A particularly promising approach is the countryside model (Pereira & Daily 2006), which outperforms alternative approaches (Pereira et al. 2014, Proença & Pereira 2013). Advantages of the countryside SAR have recently been demonstrated (e.g. Guilherme & Pereira 2013, Proença & Pereira 2013, Martins et al. 2014) yet case studies are of limited spatial extent (local to landscape scale) which enable them to use sampled data or atlas data for fitting the countryside SAR model. However, at continental scales such data are lacking or uncertain.

In order to improve our understanding of the complex land-use-biodiversity interactions at regional to continental scale, we propose a new approach to parameterize a countryside SAR and use this model to assess the distribution of plant species richness for Europe. To parameterize our model, we synthesized results from two previous studies, a biome-specific SAR for vascular plants (Gerstner et al. 2014a) and a meta-analysis of land-use effects on vascular plants (Gerstner et al. 2014b). Specifically, Gerstner et al. (2014a) found that SAR parameters vary considerably across biomes, suggesting that regional to continental-scale drivers are key determinants of broad-scale species richness patterns. In addition, Gerstner et al. (2014b) showed significant effects of land use on the species richness of vascular plants when relying on local-scale species assemblages.

We used these findings here for correcting species pool size at broad scales (50 x 50 km²) while accounting for local land-use effects (1 x 1 km²) when building our continental-scale countryside SAR model. We then compared our results with the potential species richness patterns predicted by the biome-SAR in terms of species gains and losses within our 50 x 50 km² gridcells. We validated our approach by comparing our predictions with data on plant species distributions in Europe from the Atlas Flora Europapaeae (AFE; Jalas & Suominen 1972-1994, Jalas et al. 1996, Jalas et al. 1999, Kurrto et al. 2004). In addition, we estimated prediction uncertainty due to parameter uncertainty and uncertainty due to the selection of land-use datasets.

MATERIALS AND METHODS

Study Area

Europe is an intensely studied region, i.e. a majority of ecological case studies are located in Europe (Martin et al. 2012) and large amounts of high quality land-use data are available. As these are often produced on behalf of the European Union its coverage is often limited to member states. Hence, we restricted our study area to the territory of the European Union (EU27, i.e., the EU excluding Croatia). This area is characterized by strong environmental gradients, from the boreal to the Mediterranean, and from the Atlantic climate in the West to more continental climate in the East (Fig. 1).

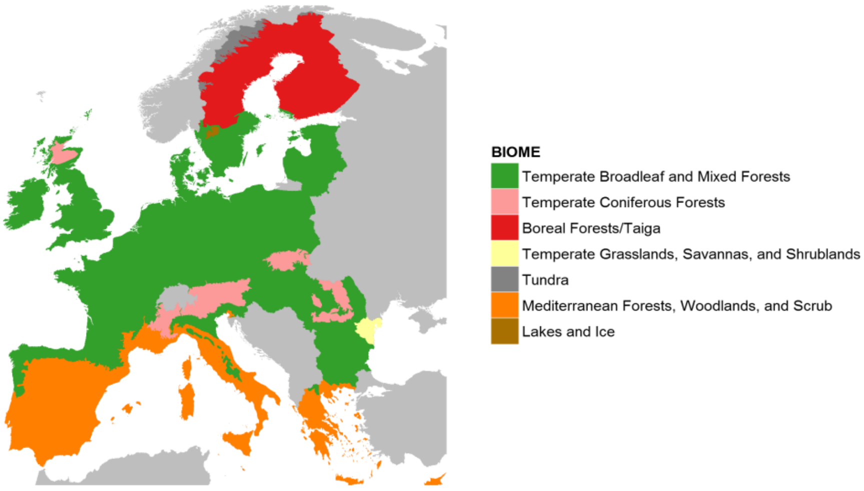


Figure 1 Distribution of biomes within the EU27 countries. Grey shadings show surrounding terrestrial area not covered by the EU27.

Species Area Relationship Models

The classic SAR assume an increase in species richness *S* with increasing sample area *A* and is mostly approximated by a power law or a linear curve in the log-log space with the parameter *c* (intercept) and *z* (slope):

$$S = cA^z \qquad (1)$$

We account for geographic variation in SAR-parameters using biomes as these have been shown to be the best geographical determinants of SARs at the global scale (Gerstner et al. 2014a). The biome-specific SAR model is as follows:

$$\log_{10}S = \sum_i(\log_{10}c_i + z_i\log_{10}A)\cdot\%B_i \qquad (2)$$

where *i* denotes the biome, i.e. c_i, z_i are SAR parameters and $\%B_i$ is the percentage of area covered by the biome B_i, hence $\sum_i \%B_i = 1$.

The countryside SAR accounts for the conservation value of transformed habitat by introducing a parameter h_i reflecting the habitat affinity of a species group to habitat type *i*, which basically is the proportion of area that can be effectively used by the species group and can be determined using a response ratio (*RR*), i.e. the ratio between species richness on land used and on original habitat, and the slope *z* of the SAR: $h_i = \left(\frac{S_i}{S_{orig}}\right)^{1/z} = RR^{1/z}$. A basic countryside SAR is formalized as:

$$S = c\cdot\left(\sum_i h_iA_i\right)^z \qquad (3)$$

Finally, we combined both models, the biome-specific SAR (eqn. 2) and the basic countryside SAR (eqn. 3) and used the following equation (4) to predict species richness pattern:

$$\log_{10}S = \sum_i(\log_{10}c_i + z_i\log_{10}\sum_j h_{ij}A_{ij})\cdot\%B_i \qquad (4)$$

Estimation of the response ratio corresponding to land use in Europe

In order to estimate the *RR* corresponding to land use in Europe, we analysed a subset of data originally collected for a global meta-analysis (Gerstner et al. 2014b, n=113 providing mean and variances for land-use and control groups). For prediction purposes, we only included significant effects, i.e. effects for which 95% CIs do not intersect 1 (Fig. 2). These were silviculture, plantation, fertilization and abandonment.

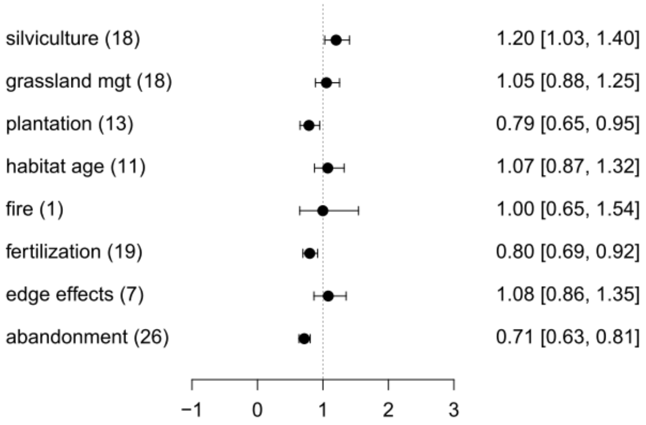


Figure 2: Effect-size plot from the linear mixed-effects model considering land-use classes as fixed effects. Dots and bars represent mean effect sizes and their 95% CI as estimated from the model. Effect sizes are response ratios and indicate the direction and magnitude of the effect of land use on plant species richness. Effect sizes greater than one suggest land use is associated with increases in species richness, whereas effect sizes smaller than one indicate decreasing species richness with increasing land use intensity. The number of study outcomes is given in brackets. For more details on the definition of land-use classes cf. Gerstner et al. (2014b).

Datasets used

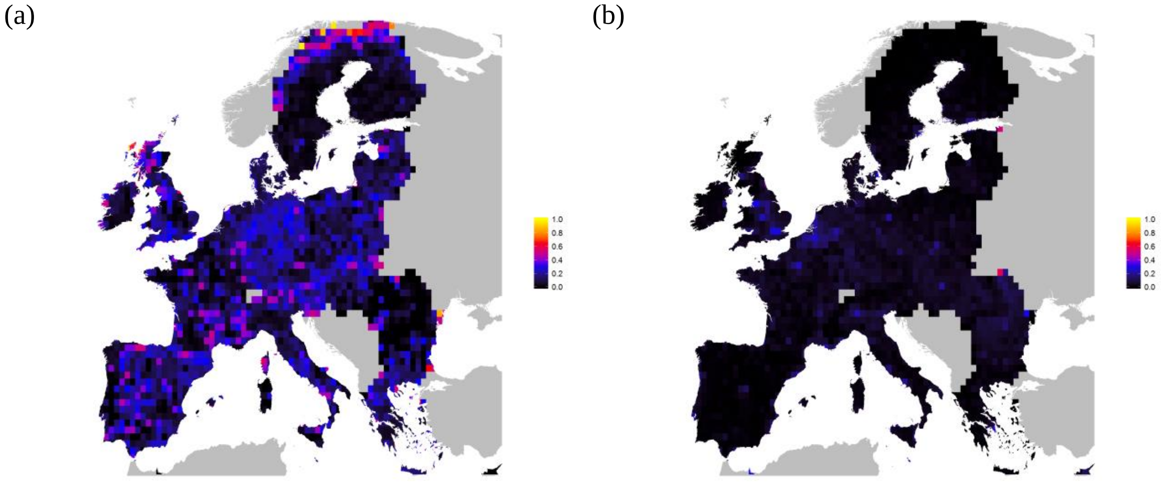
For the estimation of biome-specific SARs, we used global species richness data of vascular plants derived from floras, checklists and other literature sources for 1,032 geographical units representing natural or administrative units, such as countries or protected areas (cf. Gerstner et al. 2014a, Kreft & Jetz 2007).

In order to validate our countryside SAR model, we used plant species range maps from the volumes 1-13 of the AFE (Jalas & Suominen 1972-1994, Jalas et al. 1996, Jalas et al. 1999, Kurrto et al. 2004) which provides presence maps of vascular plant species within gridcells of 50 x 50 km² in a modified Universal Transverse Mercator (UTM) system. We projected the AFE distribution maps onto the 50 x 50 km equal-area grid (Eckert IV projection) used throughout the study. To do so, we intersected both grids and calculated species richness within 50 x 50 km² equal area grid cells.

We used land-use datasets which fitted best to how land-use classes were defined in Gerstner et al. (2014b). These datasets (Table 1) stem from different sources and therefore vary in their resolution and extent. We restricted the analysis to the extent of the agricultural intensity map (Temme & Verburg 2011) as it has the smallest extent, i.e. EU27 countries (cf. Fig.1). For the analysis, we homogenized all data for our equal area grid of 50 x 50 km². First, we intersected the biome map (Fig.1) with the equal area grid, and afterwards we intersected this biome-grid map with our land-use layers and corrected for possible overlaps between land-use data sets to avoid double-counting of areas. As reference year for the land-use layers we used 2006, except we used the Corine 2000 map as for Greece the Corine Land cover 2006 map was not available. Details on the data preparation steps, and maps of the individual land-use datasets are available in Fig.3 and in the Supplementary Material S1-S4.

Data	***Description***	***References***	***Spatial resolution***	***Temporal resolution***
Potentially manageable area	Biomes	*Olson et al. (2001)*		
	Protected areas	*EEA (2011)* *EEA (2013)*	*1 km²*	*2006*
	Land cover	*EEA (2014)*	*100 m²*	*2000*
Silviculture / Plantation	Forest cover	*Gunia et al. (2011)*	*1 km²*	*2006*
	Share of plantation species (1) Robinia spp., Populus spp., Eucalyptus spp., Pinus pinaster, i.e. tree species commonly used for timber production (2) Robinia spp., Populus spp., Eucalyptus spp., Pinus pinaster, i.e. tree species commonly used for timber production including pine (Pinus sylvestris) and spruce (Picea spp.)	*Brus et al. (2012)*	*1 km²*	*2006*
Fertilization	Nutrient input, i.e. cover of fertilized fields (grassland or cropland) using a threshold of 50 kg/ha	*Temme & Verburg (2011)* *Stürck et al. (2015)*	*1 km²*	*2006*
Abandonment	(1) abandoned agricultural areas, i.e. cropland, grassland used in 2000-2006 but not used 2006-2012 (2) permanent fallows, i.e. areas classified as farmland (in CORINE/GlobCORINE) but actually not used in 2001-2012	*Estel et al. (2015)*	*1 km²*	*2000-2012*

Table 1 Datasets used in the analysis.



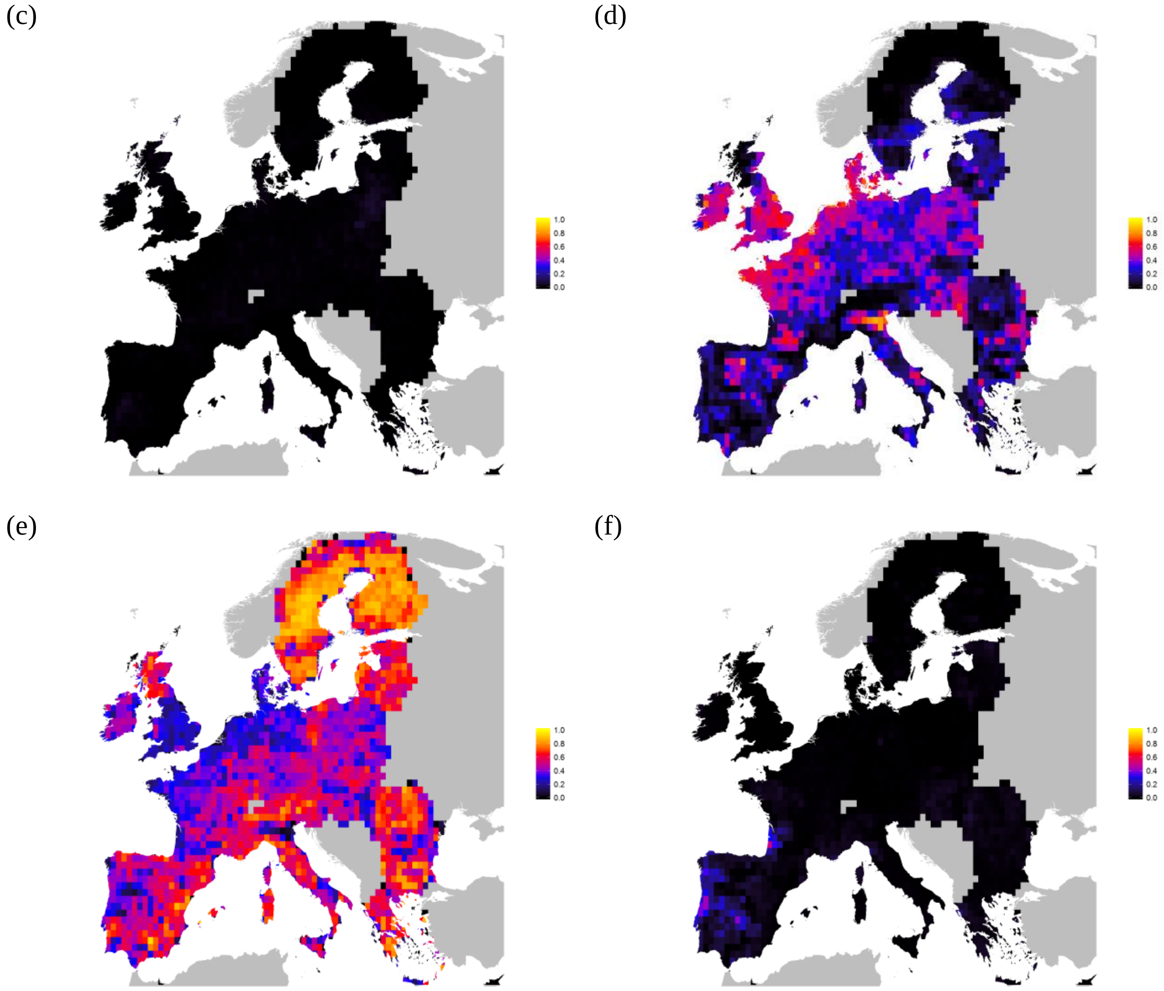


Figure 3 Example set of rastered land-use indicators aggregated to 50 x 50 km gridcells. (a) Protected areas, (b) aggregated CLC classes artificial areas, and (c) abandonment 1, (d) fertilization, (e) silviculture 1, and (f) plantation 1 corrected for overlap

Comparative Analysis

According to the different definitions of silviculture/plantations and abandonment we calculated predictions using different combinations of land-use datasets, i.e. Silviculture / Plantation 1 – Abandonment 1, Silviculture / Plantation 1 – Abandonment 2, Silviculture / Plantation 2 – Abandonment 1, and Silviculture / Plantation 2 – Abandonment 2.

We validated our approach by calculating the differences between the SAR-predictions and the species richness data from the AFE (Jalas & Suominen 1972-1994, Jalas et al. 1996, Jalas et al. 1999, Kurtto et al. 2004).

Uncertainty Analysis

We explored both model uncertainty and the uncertainty due to the selection of particular land-use datasets. To assess model uncertainty, we carried out a comprehensive analysis of parameter uncertainty. We merged two models with parameters both facing uncertainty. Although both sets of parameters are independent, parameters corresponding to one model are not. Using Monte Carlo simulation we sampled parameter sets from a multivariate normal distribution using parameter estimates and the estimated variance-covariance matrix as distribution parameters. We constrained slope parameter of biome-SAR curves to be positive, as negative slopes are theoretically possible (as samples are assumed to be independent) but are practically very unlikely especially within biomes with relatively homogeneous vegetation. We presented maps of medians and interquartile ranges to cope with outliers which were caused by the fact that mathematically habitat affinity h tends to infinity as the slope z tends to 0 when $RR>0$. Except these outliers both mean and median were comparable.

As land-use classification in Gerstner et al. (2014b) was rather broad and thereby leaving degrees of freedom for the particular choice of land-use datasets for a specific category we studied the effect of our selection. To do so, we used different sets of land-use combinations (according to the descriptions in Table 1) which all fit our broad land-use classification and calculated means and standard deviation of species richness predictions.

In addition, land-use data have their own uncertainty (e.g. classification accuracy) that is estimated and discussed in the respective papers (see Table 1 for references to the individuals land use datasets).

RESULTS

Predictions of species richness

The distribution of species richness predicted by the biome SAR, i.e. without considering land use, shows patterns according to the biomes and the latitudinal and elevational gradient (Blackburn & Gaston 2003; Fig. 4 top left). Note that species richness estimates for Temperate broadleaf and mixed forests only slightly differ from Mediterranean forests, woodland and scrublands as corresponding SARs intersect around 10^3 km² (Gerstner 2014a). Furthermore species richness is lower at the edges, such as coastlines and the borders of the EU27 countries, which is an artefact of the data resolution (i.e., EU27 territory only partially covered by our 50 x 50 km² gridcells).

In comparison, the countryside SAR predictions result in spatially more nuanced patterns (Fig. 4, Supplementary Material S5) according to the spatially varying distribution of land-use indicators (cf. Fig.3, Supplementary Material S4). We present results using the combination silviculture / plantation 1 – abandonment 1 (cf. Table 1) in the main manuscript while put the others in the Supplementary Material S5. Using this combination the countryside SAR predicts on average species gains (i.e. mean delta species richness is significantly greater than zero, cf. Fig. 4 bottom right). Overall, we note a few larger regions with biodiversity losses in Portugal, the Pyrenees, the Provence, Italy, Romania, and Slovakia.

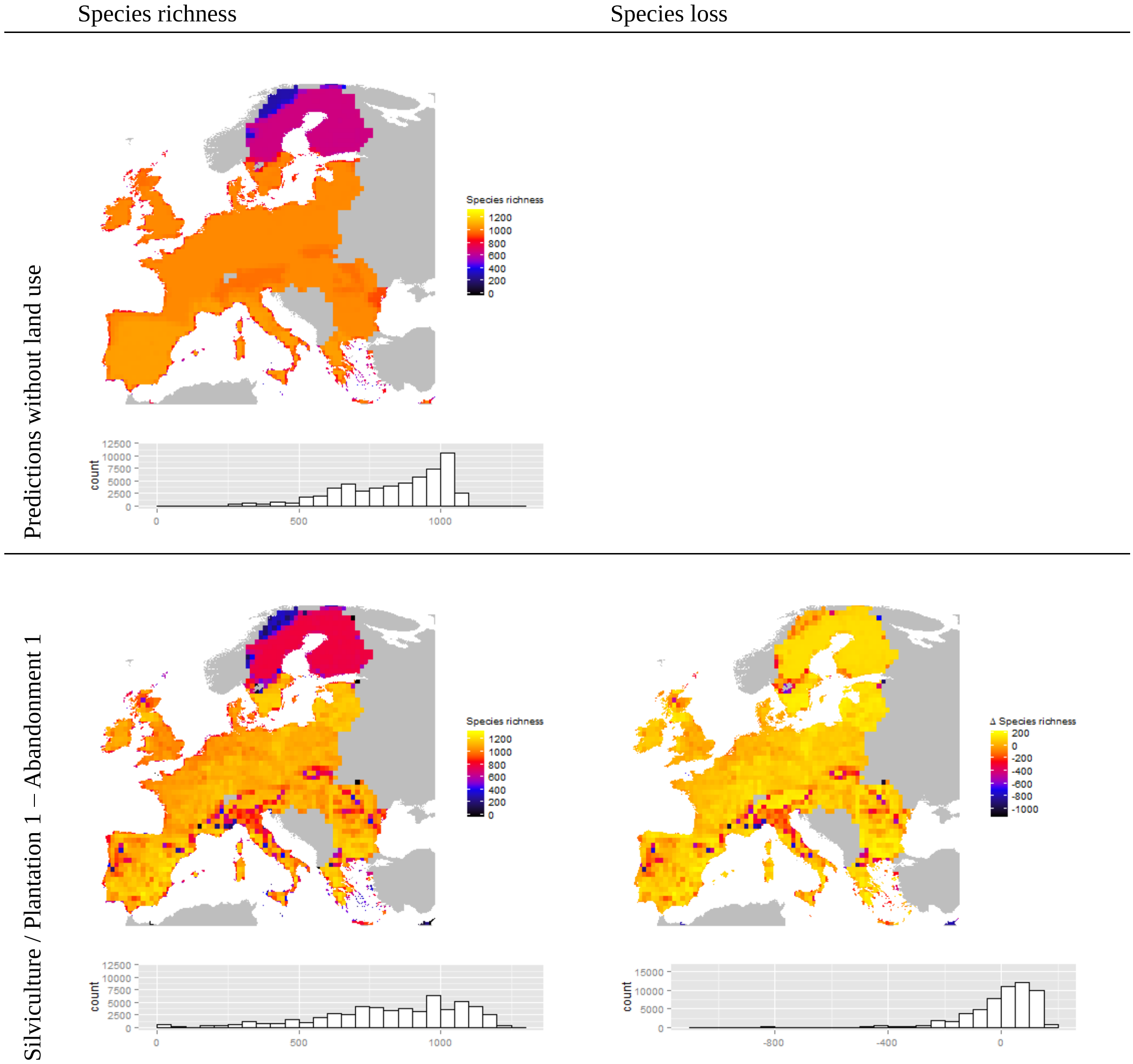


Figure 4 Predictions of species richness from the biome SAR without land use (top left) and countryside SARs using one combination of land-use data (left-hand side) and species losses and gains due to land use calculated as the difference between species richness from the countryside SAR and the biome SAR. For the purpose of comparability scales have been standardised.

Comparison with the Atlas of Flora Europaeae

Predictions of plant species richness in Europe based on our SAR-models were generally higher than in our reference dataset, the AFE (Fig. 5). This is not surprising since the AFE only covers about 20% of the known European flora (Kalwij et al. 2014). However, we also noticed regional variation and some regions with the contrary phenomenon for the countryside SAR (Fig. 5b). For example, species richness in the region around the Alps and Norway are predicted to be lower than in the AFE.

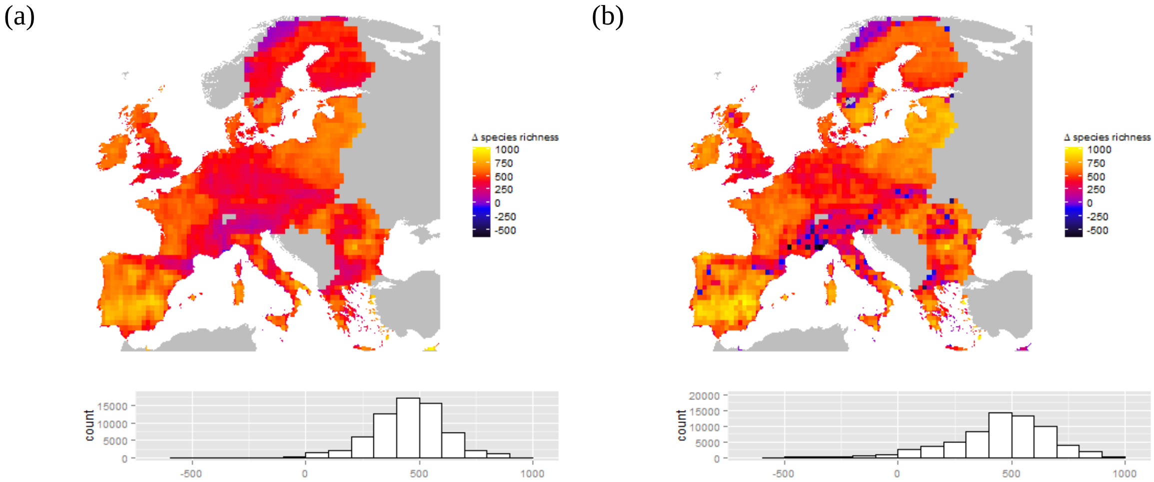
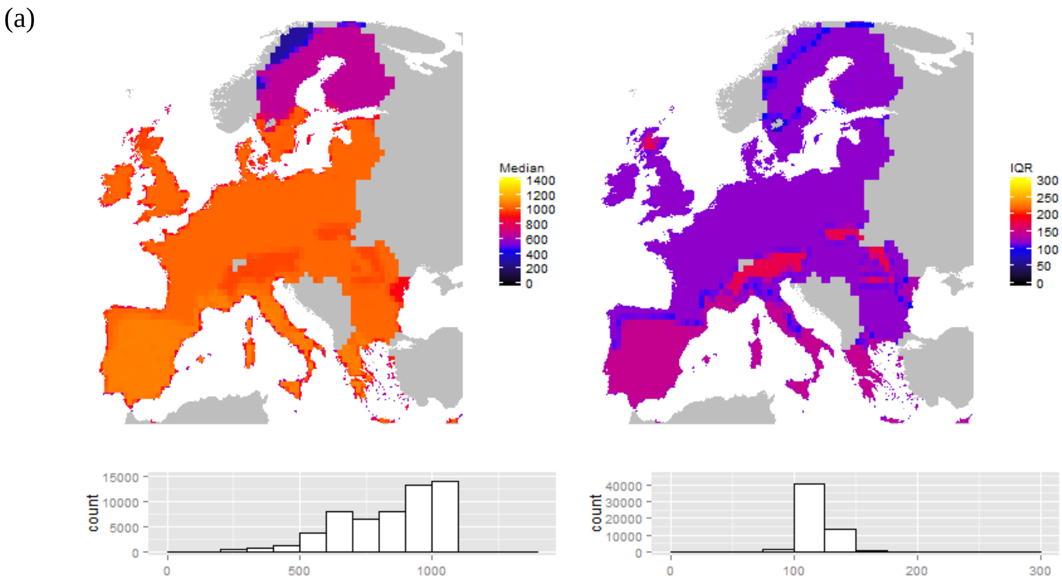


Figure 5 Comparison between species richness predictions by (a) the biome SAR and (b) the countryside SAR using the combination silviculture / plantation 1 – abandonment 1 and AFE. Positive values suggest higher predictions from the SAR-models.

Uncertainty Analysis

The uncertainty map for the biome SAR basically reflects the effects of uncertainty in SAR-parameters (Fig. 6a). For example, the high uncertainty of species richness predictions in the biome “Temperate coniferous forest” results from the uncertainty of the SAR-slope within this biome (Gerstner et al. 2014a). In addition, uncertainty in the predictions of species richness from the countryside SARs (Fig. 6b, S6.2-S6.5 in the Supplementary Material) depends on the uncertainty of the response ratios (cf. Fig. 2). For example, response ratios for plantations and silviculture show relatively high variation causing that the ratio of IQR/Median is relatively high in regions with high coverage of plantations and silviculture, e.g. Norway and the Alps.



(b)

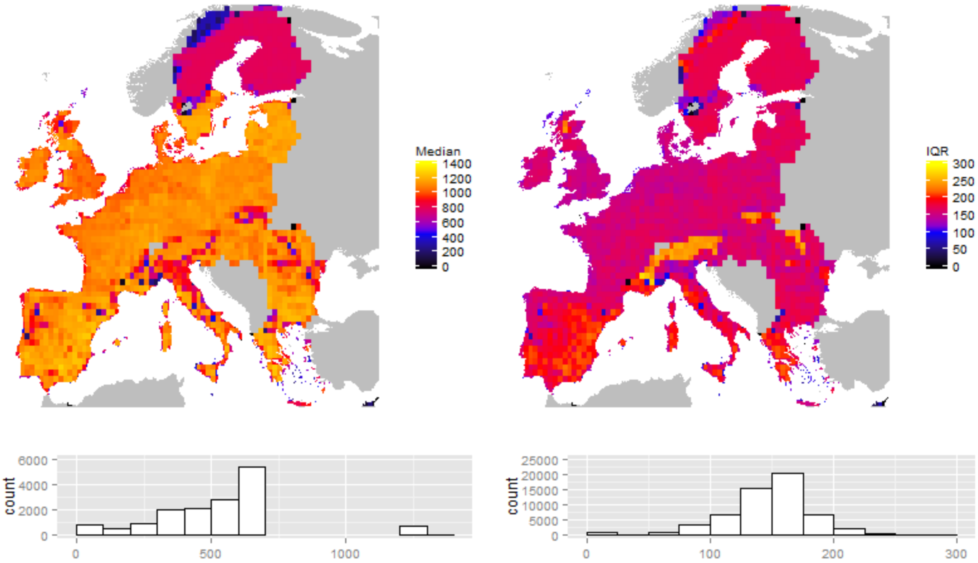


Figure 6 Uncertainty maps of species richness estimates based on (a) the biome SAR, (b) the countryside SAR using the combination silviculture / plantation 1 – abandonment 1.

The uncertainty analysis further shows large regions where estimates are relatively unaffected by the choice of the land-use-indicator combination, i.e. predictions are consistent over all sets of land-use combinations (Fig. 7). These regions are covered by high percentages of land use which negatively affect species richness such as fertilization, abandonment, and plantation compared to the cover of protected areas, and silviculturally managed forests.

On the other hand, definitions and combinations strongly determines the reliability of estimates in Eastern Europe (mainly due to abandonment) and in Sweden and northern Spain (mainly due to plantation / silviculture, cf. Fig. 3, Fig. S4 in the Supplementary Material). These differences are a result of differences in land-use indicators: Abandonment 2 includes more areas than the narrower definition of abandonment 1 and is mostly in the mountainous regions of the Alps and Eastern Europe (cf. Supplementary Material S2-S4). In these regions, some areas have lower species richness estimates when considering permanent fallows instead of abandonment but the overall picture does not change (cf. Supplementary Material S5). Furthermore, silviculture / plantation 2 includes pine and spruce stands as plantations. Hence, more areas are designated to be negatively affected by plantations, while at the same time pine and spruce stands are sometimes naturally occurring rather than silviculturally managed forests. As a result, species richness estimates of the combination plantation / silviculture 2 are lower compared to plantation / silviculture 1 (Supplementary Material S5).

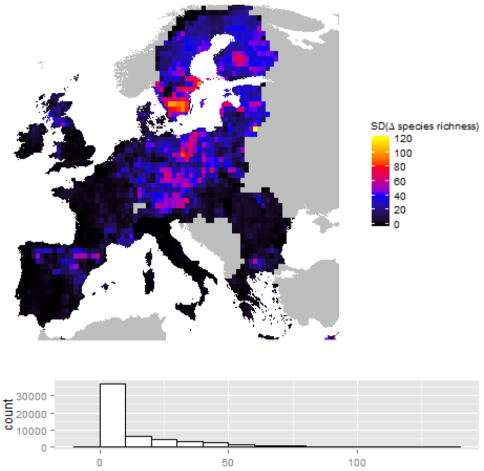


Figure 7 Map of uncertainty due to different combinations of land-use indicators (cf. Table 1), shown as standard deviation of predictions of species richness change across the four countryside SARs.

DISCUSSION

Land use is a crucial determinant of species richness pattern and thus need to be considered in models of biodiversity change. Especially at the regional scale, where the level of endemism is high and usually decisions about external factors and the allocation of conservation funds are made (e.g. EU CAP, NATURA2000), improved predictions are needed about how land use have changed and will change biodiversity. Here, we presented an improved, broad-scale SAR-approach for vascular plants that consider both environmental variation and the conservation value of the countryside, and made predictions about biodiversity changes at regional to continental scales. This countryside SAR model predicted spatially more nuanced patterns according to the spatially varying distribution of land-use indicators compared with a SAR approach which only accounted for environmental correlates, such as biomes, and diregards land use. In comparison with the AFE, our SAR approaches predicted generally higher species numbers, whereas there were also areas where the countryside SAR predicted lower species numbers than the AFE. Despite limitations and uncertainties, the countryside SAR is a very flexible approach to predict changes in biodiversity distribution due to land use and we suggest how our model can be further improved.

While other existing models of species richness changes based on SARs (e.g. Van Vuuren et al. 2006) assume a single outcome of land use on richness, that is the net loss of area due to agricultural conversion and a net gain due to abandonment, our countryside SAR approach considers the complex and multidimensional effects that land use has on plant species richness. Another widely known model assessing land-use changes on biodiversity at global scales is the GLOBIO model (Alkemade et al. 2009) which uses however mean species abundances (MSA) as a biodiversity indicator. MSA represents the average response of the total set of species belonging to an ecosystem. Hence, the GLOBIO model is restricted to the response of original species ignoring that with land use new species might add to the original community. As a result land use generally show negative effects on the diversity of plants and vertebrates while the meta-analysis of Gerstner et al. (2014b) shows also positive effects (e.g. for silviculture) on plant species richness. Hence, our predictions of species loss may be comparably low since positive effects of certain land uses might level out negative effects of others. The differences in the use of biodiversity indicator and in the effects of land use between both models likely lead to quite different spatial patterns of predictions of species losses due to land use.

The AFE covers the large geographic extent of Europe, however only covers about 30% of the known European flora (Kalwij et al. 2014). Hence, it is not surprising that our predictions of species richness are generally higher (Fig. 4). Despite its incompleteness, general diversity variation in regional databases is well represented by the variation of the portion of species included in the AFE (Kalwij et al. 2014). Causes of the regional differences between our predictions and the AFE might be manifold. One cause is that the SARs predict lower species richness at the edges due to smaller cover of grid cells. However, while this might be reasonable at terrestrial-oceanic borders it is not within continents, e.g. at the border of Greece and the Balcan states (cf. Fig. 5).

A number of uncertainties in our analyses need mentioning: First, our sensitivity analysis reveals that the selection of land-use data sets is crucial (Fig. 7). For example: Though the definition of abandonment is only slightly different from permanent fallow, we noticed a completely different spatial geographic pattern (Supplementary Material S4) which highly influenced results. Furthermore, the delineation of plantation vs. silviculture had strong impacts on our results. In line with Whittaker et al. (2005), instead of producing a single map of biodiversity changes due to land use, we suggest to produce sets of alternative maps, based on varying choices of land-use indicators.

Second, it is quite reasonable to assume that there is a land-use imprint in the species richness data used to fit the biome SAR – given the long land-use history, e.g. forest transitions mainly in the 19th century. Samewise, land-use effects are likely to be determined using a seminatural rather than a natural baseline for comparison - given the long land-use history in Europe leaving few landscapes as purely natural. As such we do not expect that our results are flawed. We further assumed that protected areas are completely unmanaged or that management does not affect diversity pattern. However, different concepts are applied for the designation of protected area, so that it is questionable whether protected areas are free from management. For example, the Aquitaine region in south-western France harbours a large protected area while this region is traditionally intensively used for wood-production and characterised by a high share of plantation species (e.g. Levers et al. 2014). In contrast to protected areas we set the response ratio for artificial areas to zero, and thereby make the assumption that artificial areas, e.g. cities, do not contribute to regional diversity. A recent meta-study on urbanization effects (Aronson et al. 2014) indeed show that only 5% of vascular plant species worldwide occur in cities but still urban biotas reflect their regional biogeographic species pool and only a few cosmopolitan species occur across cities.

Moreover, it has been shown that globally biomes predict effect size variation in addition to land-use (Gerstner et al. 2014b). However, due to data limitations we could not fit additive effects of land-use and biomes at the European scale. In order to overcome this limitation, more case studies need to be involved in the meta-analysis.

Finally, the countryside SAR separates species into functional groups with different affinities for native and human-modified habitats (Pereira & Daily 2006). By using vascular plants as a single functional group we assume that all vascular plant species share a single response towards land use, thus revealing nothing about the relative vulnerabilities of species functional subgroups to extinction. Most likely, the relationship will vary depending on the niche width of species in the community: specialist species (narrower niche) will be more affected by declining habitat size and habitat number increases than generalist species (wider niche, Martins et al. 2014). Using the approach of Proença & Pereira (2013) one could distinguish between three functional groups of vascular plants, which are agricultural species, shrubland species and forest species.

Despite its limitations and uncertainties, we have presented a very flexible approach to predict changes in biodiversity distribution due to land use. It especially overcomes unrealistic assumptions of previous model approaches (e.g. Van Vuuren et al. 2005, Alkemade et al. 2009) about constant and general negative effect of land use. Integrating varying land-use effects into a SAR-model enable predictions about the combined effects of land use and hence give a much more spatially nuanced picture than the classic SAR-model. Moreover, such a broad-scale approach allows the study of scenarios and trade-offs resulting from national and international policy changes. Forthcoming studies can contribute to its improvement, e.g. by updating land-use effects on species richness and providing better maps for land-use indicators. Moreover, vascular plant species richness has been the core taxa for land-use assessments, mainly because of data availability and the close association to specific land uses, nevertheless the approach can be applied to other taxa as well.

Further investigation and validation of predictions such as hotspots of species losses would contribute to the question whether we missed some important mechanisms, e.g. land-use classes. Furthermore, we found meta-analysis particularly useful for quantifying effects of land use on species richness and these data can be easily supplemented and analysis repeated to refine results. To increase the number of case studies used to quantify response ratios more focussed searches may be useful (e.g. in grey literature and considering other languages). This would further help to study contrasting results, which we, for example, found for the effects of abandonment in Europe: Plieninger et al. 2015 show on a more local scale that land abandonment in the Mediterranean basin slightly increase plant species richness.

In this study Europe has been used as a showcase as it is a highly investigated region with high numbers of case studies on land-use effects on species richness (Gerstner et al. 2014b) and a wealth of available high-quality land-use datasets. However, the presented approach can be also transferred to other regions, where the collection of such data is feasible, and supplemented by integrating other effects of other land-use indicators. In the future there might be even global land-use datasets available (Kuemmerle et al. 2013) ensuring consistency in scenario evaluation. This is particularly important as drivers influencing individuals' land-use decisions increasingly act at continental to global scales (e.g. Lambin & Meyfroidt 2011).

CONCLUSION

Recent models of environmental change include land use as equivalent to habitat loss. However, land use effects are much more variable. In order to consider the conservation value of the countryside, a modification of the SAR approach has been suggested – the countryside SAR – but yet has so far been only applied at local to landscape scales where sampled data or atlas data were available. We have presented a promising approach which integrates both environmental variation as well as land use into models of biodiversity distribution. This broad-scale approach which integrates fine-scaled mechanisms, such as land use, with broad-scale species richness patterns will improve predictions of environmental change and better inform environmental policy at the scale of regions to continents.

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SUPPORTING INFORMATION

Appendix S1 - Concrete steps of data preparation

Appendix S2 - Maps of source layers

Appendix S3 - Maps of transformed layers

Appendix S4 - Rastered land-use indicators

Appendix S5 - Predictions from countryside SARs

Appendix S6 - Uncertainty of species richness estimates due to parameter uncertainty

Author contributions: K.G., T.K. and R.S. conceived and designed the project; C.L. gathered the land-use data; K.G. analysed the data and led writing; all authors contributed to revisions.

3.4 Other Publications

In connection with this dissertation several other co-author publications has been published or submitted:

Magliocca, N.R., Rudel, T.K., Verburg, P.H., McConnell, W.J., Mertz, O., Gerstner, K., Heinimann, A. & Ellis, E.C. (2014) Synthesis in land change science: methodological patterns, challenges, and guidelines. Regional Environmental Change, 1–16.

This publication arose in the context of the workshop "Land Change Meta-analysis: Expert Experiences & State of the Art" held from May 16-17 2012 in Amsterdam, NL. Meta-studies in land change science encompass a variety of methods. Meta-analysis of effect sizes is one of those methods and with my in-depth knowledge (cf. Gerstner *et al.*, 2014b, which was not yet published at this point of time) I was particularly able to contribute to the workshop content and the publication.

Stein, A., Gerstner, K. & Kreft, H. (2014) Environmental heterogeneity as a universal driver of species richness across taxa, biomes and spatial scales. Ecology Letters, 17, 866–880.

In my dissertation I focussed on the study of habitat area, land use and intensification effects. However, it is also widely acknowledged that environmental heterogeneity is a highly important factor governing species richness patterns. Both meta-analyses, i.e. Stein *et al.* (2014); Gerstner *et al.* (2014b) were conducted in close cooperation especially with regard to technical issues.

Seppelt, R., Beckmann, M., Ceauşu, S., Cord, A.F., Gerstner, K., Gurevitch, J., Kambach, S., Klotz, S., Mendenhall, C., Phillips, H.R.P., Powell, K., Verburg, P.H., Verhagen, W., Winter, M., Newbold, T. (submitted) Harmonizing Biodiversity Conservation and Productivity in the Context of Increasing Demands on Landscapes, Bioscience

As society strives to achieve food and energy security alongside biodiversity conservation goals, it becomes crucial to study the effects of land-use on both biodiversity and provisioning ecosystem services. This general conceptual framework aims to link biodiversity and agricultural production through the separate relationships between land use and biodiversity, and between land use and production. Among other publications the meta-analysis of Gerstner *et al.* (2014b) has been cited as available evidence for the relationship between land use and biodiversity and thus served as a key reference for the proposed framework.

Kehoe, L., Senf, C., Meyer, C., Gerstner, K., Kreft, H. & Kuemmerle, T. (in prep.) Land cover and land-use intensity rival biomes in predicting global species richness

In today's human dominated world, large-scale patterns of mammal species richness might be shaped by human activities more than by environmental covariates such as biomes. Using recently available global scale datasets, it was assessed how SARs vary with biomes, land cover and land-use intensity. In contrast to Gerstner *et al.* (2014a) it has been found that land-cover and land-use intensity perform as well as biomes in predicting SAR-patterns. Using similar methodology as in Gerstner *et al.* (2014a) this study served as an extension of the work presented in this dissertation.

CHAPTER 4

Synthesis

4.1 Distribution of native plant species richness at the global scale

The species–area relationship is one of the most intensely studied patterns in ecology and is often used to map species richness patterns. Therefore, it is required to adequately define model parameters. It has been shown that incorporating geographic variation into the otherwise simple model leads to considerable improvement of the prediction of species richness patterns (cf. Gerstner *et al.*, 2014a). For the analysis the best available global species richness data for vascular plants have been used. As possible determinants of geographical variation in SARs biogeographical provinces were chosen: Floristic kingdoms as surrogate for evolutionary history, biomes as surrogate for both evolutionary history and ecosystem productivity, and land cover as a surrogate for habitat diversity. The best model accounted for variation due to biomes and explained almost half of the species richness variation. The results suggest that ecosystem productivity and evolutionary history, both captured in biomes, mainly determine the patterns of plant species richness at the global scale. The global map of native plant species richness (Fig. 4b in Gerstner *et al.*, 2014a) well displays the well known latitudinal species richness gradient. The study illustrates specific patterns in global SARs and how our understanding of these patterns is advancing. Evidence of systematic variation between biomes suggests that the use of canonical z values (e.g. 0.25) in classic SARs to estimate extinctions resulting from habitat loss is likely to result in erroneous predictions. Such insights are of particular importance to improve conservation guidance (Whittaker & Matthews, 2014). In particular, using biome-specific SARs it is possible to predict climate change effects on plant species richness distribution if it is assumed that climate change leads to a shift in the distribution of biomes (Millenium Ecosystem Assessment, 2005).

4.2 Effects of land use on plant diversity

Plant diversity is globally threatened yet evidence from numerous case studies at regional and local scales is mixed. Much of the current disagreement comes due to the variety of land-use options being examined in various regions and at various temporal and spatial scales, hampering direct comparisons of studies. Furthermore, land use indirectly affects remaining native vegetation, and specific effects might generally depend on the environmental, historical and socio-economic context. Using a meta-analytic framework and a global dataset extracted from 375 studies the effects and their variation of 11 classes of land use were studied. The analysis unequivocally demonstrates that land use matters, but that its effects on plant species richness substantially vary: Although most human land uses appear to have negative effects on plant species richness, the specific type and location of land use are crucial considerations (Fig. 3 in Gerstner *et al.*, 2014b). For example, positive associations between silviculture and prescribed fire with plant species richness have been detected which can be attributed to mechanisms that directly support species coexistence and persistence. Further, variation of effects was best explained by land-use specific covariables (Fig. 4 in Gerstner *et al.*, 2014b) but generally land-use effects differ between biomes suggesting that in regions with larger species pools, the impacts of land use on species richness tend to be lower (Figs. 5 and 6 in Gerstner *et al.*, 2014b). This particular result suggests that in regions with large species pools, species that are negatively impacted by land use are perhaps more readily exchanged with others from the species pool. This extensive synthesis helps to overcome one of the most important debates in the ecological literature - how the global biodiversity loss relates to smaller spatial scales and how it is moderated by land use (Bennett, 2014).

4.3 Integrating land use into broad-scale species richness pattern using a countryside SAR approach

Recent models of environmental change include land use as equivalent to habitat loss (e.g. Alkemade *et al.*, 2009; Van Vuuren *et al.*, 2006; Millenium Ecosystem Assessment, 2005). However, land use effects are much more variable (cf. Gerstner *et al.*, 2014b) and accounting for the conservation value of the countryside is crucial to improve predictions of environmental change. The countryside SAR, as a modification of the classic SAR which consider the conservation value of the countryside, yet have been only applied at small scales where sampled data or atlas data were available. As such data is scarce at continental scales, a countryside SAR which integrates both environmental variation as well as land use into models of biodiversity distribution was presented and tested at the example of Europe. Overall, this countryside-SAR approach overcomes the unrealistic assumptions of previous model approaches about constant (Van Vuuren *et al.*, 2006; Millenium Ecosystem Assessment, 2005) or general negative effects of land use (Alkemade *et al.*, 2009). Integrating varying land-use effects into a SAR-model enable predictions about the combined effects of land use and hence give a much more spatially nuanced picture than the classic SAR-model. The methodological crux of this study was to combine findings from a global SAR study and from a meta-analysis (Gerstner *et al.*, 2014a,b) in order to parameterize the model.

4.4 Challenges and limitations

Land use and changes therein interact with biodiversity across spatial scales. While effects of specific land-use types have mostly been observed at local scales covering a range from 0.1 m^2 to 1000 km^2 (Gerstner *et al.*, 2014b), the collective broad-scale impacts of various land-use types within the same matrix might be different. Furthermore, drivers of land use increasingly act at regional to global scales as a result of globalization amongst other reasons (Lambin & Meyfroidt, 2011). Hence, a broad-scale perspective is needed to improve predictions about how land use have changed and will change biodiversity and to use them to inform environmental policy. Such a broad-scale perspective, however, is particularly challenging due to various reasons:

1. The global distribution of land use and its change shows large regional differences (Ellis *et al.*, 2013). Moreover, specific types and effects of land use vary regionally (Gerstner *et al.*, 2014b) hampering the development of a consistent land-use classification scheme and appropriate maps of land-use indicators. In addition, technical challenges remain to map global land use (Kuemmerle *et al.*, 2013), e.g. fine-scale land-use data with global coverage remains scarce, as data needed to produce them are frequently only available at national or sub-continental scale; existing datasets are often inconsistent in time, space, or map legends and require substantial homogenization effort; uncertainties in land-use datasets are often high or remain unquantified because formal validation is lacking; dataset construction often relies on covariates which may result in inducing endogeneity in subsequent problems; disaggregation of spatial resolution of coarse-scale land-use datasets results in substantial bias in area estimates. A better characterization of the spatial patterns of global land use is crucial to study its impact on biodiversity and to understand the drivers of its change (Kuemmerle *et al.*, 2013).

2. The second challenge is related to the Linnaean shortfall: plant species richness data come from historical sources (Kreft & Jetz, 2007; Kalwij *et al.*, 2014) and may be either incomplete or fail to reflect current knowledge (Ladle & Whittaker, 2011). Other plant distribution data are sparse and only exist at a regional scale. Merging of species distribution datasets has been proposed to fill gaps in our floristic knowledge (Kalwij *et al.*, 2014) yet have to be undertaken. Moreover, recently a project started which aims at merging vegetation-plot databases worldwide (sPlot) and therewith contribute to the increase of global floristic knowledge.

3. The term biodiversity encompasses the variety of genes, species and ecosystems. Using species richness as an indicator of biodiversity had several reasons: it is the most widely used measure of ecosystem performance and commonly hypothesized to support ecosystem functioning (Hooper *et al.*, 2005; Isbell *et al.*, 2011); theories about determinants of species richness exist at a wide range of spatial scales (Turner & Tjørve, 2005; Storch *et al.*, 2007; Blackburn & Gaston, 2003) making it possible to build predictive models across scales; data availability (e.g. distribution data, species lists) is relatively good compared to other diversity indicators for which abundance data might be needed. However, species richness change is just one part of the bigger picture of biodiversity change including alterations of distribution, composition, and abundance. For example, although absolute numbers of species might not be affected, a considerable amount of species may be lost and replaced by a small number of widespread, human-adapted species (van Kleunen *et al.*, 2015). This form of species replacement is of concern because it results in a reduction in genetic diversity and homogenization of floras (Millenium Ecosystem Assessment, 2005; Sax & Gaines, 2003).

4. Meta-analysis has been shown to be particularly useful to synthesize local-scale findings about land-use effects on biodiversity. However, findings are likely to be biased, when studies are unevenly distributed across the globe. Geographical bias of applied ecological studies has been reported repeatedly (Martin *et al.*, 2012; Gerstner *et al.*, 2014b). Most notably is the bias towards high-income nations within Europe and North America. However, it is unclear whether this pattern will remain when literature searches are extended towards the inclusion of non-english publications and grey literature (i.e. research studies not published in scientific journals).

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https://www.idiv.de/sdiv/workshops/workshops_pool/splot.html

4.5 Conclusion and prospect

The here presented work has shown that land use plays a major role in determining species richness pattern worldwide and that it is crucial to consider the collective impacts of land uses at broad scales in order to improve predictions of environmental change and evaluate spatially explicit future land-use scenarios in terms of species richness losses and gains. Such scenario evaluation has been shown to be a useful tool to investigate options for reducing global biodiversity loss (Millenium Ecosystem Assessment, 2005; Van Vuuren *et al.*, 2006; Alkemade *et al.*, 2009). The here presented countryside SAR-model is a fundamental improvement of previous models which for simplicity assumes that the diversity of human-dominated vegetation is zero and that abandonment of agricultural land results in immediate habitat gain (Van Vuuren *et al.*, 2006; Millenium Ecosystem Assessment, 2005). Compared to the well-known GLOBIO3 model (Alkemade *et al.*, 2009) the countryside SAR-model also has been based on cause-effect relationships found using a meta-analysis. However, results are hardly comparable as biodiversity indicators differ – GLOBIO3 used mean species abundance which represents the average response of the total set of species belonging to an ecosystem. Hence, the GLOBIO3 model is restricted to the response of original species ignoring that with land use new species might add to the original community. As a result land use generally show negative effects on biodiversity while the meta-analysis of Gerstner *et al.* (2014b) shows also positive effects, e.g. for silviculture, for plant species richness. Moreover, as in GLOBIO3 climate change effects can be considered via forecasts of biome shifts.

Human-induced land transformation and the resulting changes of ecosystems are the direct result of human decision-making at multiple scales (Meyfroidt *et al.*, 2013). Studying the linkages between globalization, actual land-use changes and environmental impacts posses challenges and needs the integration of both drivers and impacts of land-use change as part of global environmental change (Turner *et al.*, 2007; Meyfroidt *et al.*, 2013). Therefore, the research field of "Land Change Science" has recently emerged and engages an interdisciplinary group of researchers across the social, economic, geographical, and natural sciences to collaborate (Verburg *et al.*, 2013). This PhD-thesis contribute to the land change science research by integrating the disciplines of macroecology, remote sensing, landscape ecology, and biogeography, amongst others. It thus serves as a showcase of how such interdisciplinary collaboration can produce scientifically and policy relevant outputs.

Specifically, the presented SAR-model enable predictions about the combined future climate and land-use change effects on the distribution of plant richness which can be used to better inform environmental policy at the scale of regions to continents. Using such predictions, conservation organizations and natural resource agencies may direct conservation efforts toward biodiversity at broad-scale and then determine the extent to which ecosystems and species at finer scales should be targeted (Poiani *et al.*, 2000). Such a progressive strategy towards an intact matrix is often key to the long-term persistence of large- and small-patch ecosystems and lower-scale species. Furthermore, predictions can be used to suggest the removal or modification of external factors that give rise to species losses (Bignal & McCracken, 2000; Poiani *et al.*, 2000).

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Selbstständigkeitserklärung

Hiermit erkläre ich an Eides statt, dass ich die vorliegende Arbeit selbständig und ohne fremde Hilfe verfasst habe, keine anderen als die von mir angegebenen Quellen und Hilfsmittel benutzt habe und die den benutzten Werken wörtlich oder inhaltlich entnommenen Stellen als solche kenntlich gemacht habe.

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