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Thesis Abstract

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

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Abstract. Plant species richness is essential for ecosystem functioning, resilience and ecosystem services, yet is globally threatened by anthropogenic land use, including management and modification of the natural environment. At broad scales, land-use effects are often simply modelled by habitat loss, assuming that transformed land becomes completely inhospitable for naturally occurring species. Further, estimates of species losses are flawed by the common assumption of a universal slope of the species–area curve, typically ranging from 0.15 to 0.35. My PhD dissertation consists of a global species–area analysis, a meta-analysis about land-use effects on plant species richness and an approach to integrate these land-use effects in a countryside species–area model. Overall, my PhD research contributes to a deeper understanding of species–area relationships and how patterns of species richness at macroscales are driven by land use. It proposes a model to predict species richness patterns of vascular plants that overcomes limitations of previous models.

Keywords: Biodiversity, conservation biogeography, Europe, land use, meta-analysis, plants, species–area relationship, species richness

Introduction

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. In particular, land use is considered a major threat to biodiversity worldwide because it leads to destruction, degradation and fragmentation of habitats (Millennium Ecosystem Assessment 2005, Pereira et al. 2012). Vascular plants are strongly linked to human land use and are of special importance for all life on Earth: generally, plant diversity is needed to maintain ecosystem functions and services, and is therefore instrumental to ecosystem health and ultimately human well-being (Isbell et al. 2011, Cardinale et al. 2012).

In order to reduce global biodiversity loss and consequent impacts on human well-being, studying ecosystem attributes and their complex interactions with land use is essential. Those studies also need to incorporate a wide range of spatial scales, for several reasons. First, land use directly affects ecosystems at local scales (Hooper et al. 2012), but biodiversity loss is typically assessed at regional and global scales (e.g. Millennium Ecosystem Assessment 2005), since drivers of land-use decisions increasingly act at regional, continental to global scales – as a result of globaliza-

tion, the industrialization of agriculture and forestry, and the increasing influence of transnational corporations (Lambin & Meyfroidt 2011). Moreover, biodiversity loss is of great concern at the regional scale, where the level of endemism is high and political decisions about the allocation of conservation funds are usually made.

The species–area relationship (SAR) is a prominent concept for predicting species richness and biodiversity loss across spatial scales and therefore has profound importance for conservation biogeography (Ladle & Whittaker 2011). This relationship describes an increase in species richness with increasing sample area. Observed SARs are mostly approximated by a power law (Arrhenius 1921) because this has been shown to describe SARs appropriately under most conditions (Dengler 2009, Triantis et al. 2012):

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

or its linear function in log–log space:

$$log(S) = log(c) + z\ log(A) \qquad (2)$$

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.

The recent debate about whether SARs are the most appropriate method to estimate biodiversity loss (He & Hubbell 2011, Pereira et al. 2012) shows that current applications of SARs to estimate species richness and its change are based on overly simplistic assumptions: first, recent models have used a limited range of model parameters, such as a fixed z-value 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), which is based on theoretical assumptions (cf. Harte & Kitzes 2012) rather than empirical analyses. Second, recent models assume that human-modified habitat becomes completely inhospitable, ignoring the fact that many species may persist. To adequately predict species richness and how it is affected by land use, it is crucial to obtain a good model fit and to consider the potential of human-modified habitat to sustain species.

The overall aim of my PhD dissertation (Gerstner 2015) was 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 better future predictions. Therefore the main research questions were:

1. Can I produce a better global SAR model to estimate the distribution of native plant species richness at the global scale by including variation due to historical, or environmental determinants?

2. How do different types of land use affect plant diversity at local to regional scales and do these effects further depend on the environmental, historical or socio-economic context?

3. How can I integrate the varying effects of land use into a SAR-model which predicts the distribution of native plant species richness?

Accounting for geographical variation in global species–area relationships

For the global SAR-analysis I used the best available global species richness data for vascular plants (Fig. 1; Barthlott et al. 2005, Kier et al. 2005; also see Kreft & Jetz 2007). These data contain species richness information within geographical units differing greatly in size (areas ranged between 13.5 km² and 575,440 km², Fig. 1b) and shape and were derived from floras, checklists and other literature sources. Therefore, this data set is likely to reflect species richness of the semi-natural vegetation, i.e. native and naturalized alien taxa, excluding recent species introductions and extinctions resulting from land use. 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.

At the macroscale, evolutionary history and ecosystem productivity (resulting from temperature, water availability and soils, among other factors) are suggested to be the most important correlates of species richness patterns besides area (e.g. Storch et al. 2007). Specifically, history and productivity drive
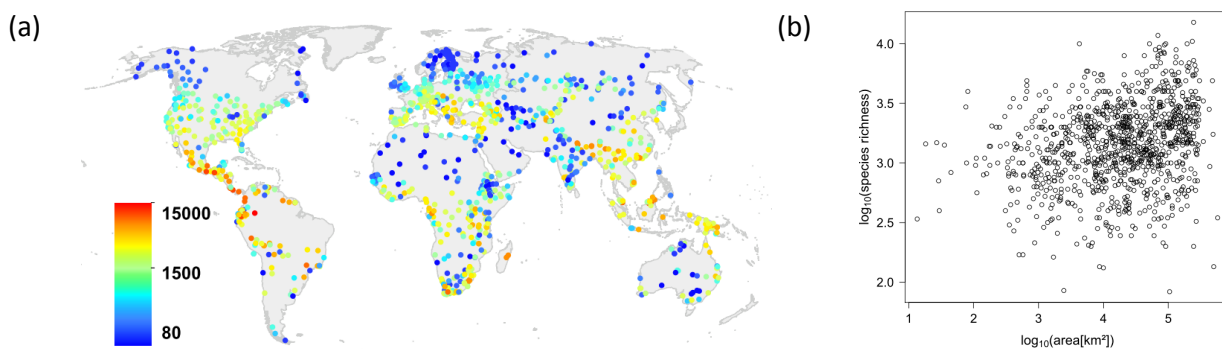
(a)

(b)

Figure 1. (a) Geographic distribution of richness data for vascular plants used in the analysis (n=1032, after Barthlott et al. 2005, Kier et al. 2005). 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) for each geographical unit in (a). Figure reproduced with publisher's permission from Gerstner et al. (2014a).

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 a review). 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. Consequently, as possible determinants of geographical variation in SARs across biogeographical provinces, I chose: floristic kingdoms as proxies for evolutionary history, biomes as proxies for both evolutionary history and ecosystem productivity, and land cover to account for both (semi)natural and human-modified habitats.

The best model incorporated variation between biomes and explained almost half of the species richness variation, in contrast to only 6% using a single global SAR (Gerstner et al. 2014a). This result suggests that ecosystem productivity and evolutionary history, both captured in biomes, mainly determine the patterns of plant species richness at the global scale. Evidence of systematic variation between biomes (Fig. 2a) 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 particularly important for improving conservation guidance (Whittaker & Matthews 2014).

This modelling approach is also easily implemented in applied studies predicting species richness patterns at appropriate scales (e.g. 100 km x 100 km, Fig. 2b). The number of species in a given area *A* can be estimated by summing up species richness estimates for each biome. The biome-specific SAR model is defined as:

$$\log_{10}S = \sum_i (log_{10}c_i + z_i log_{10}(B_iA)) \quad (3)$$

where c_i, z_i are the SAR parameters for each biome *i*, and B_i is the fraction of area covered by the biome *i*, hence $\sum_i B_i = 1$. I strongly recommend that the model is not applied at small scales at which other factors may determine variation in SARs (Turner & Tjørve 2005).

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

Plant diversity is globally threatened by anthropogenic land use, yet evidence for declining species diversity from numerous case studies at regional and local scales is mixed. Much of the current disagreement results from the variety of land-use options being examined in various regions and at various temporal and spatial scales, hampering direct comparability of studies. Furthermore, land-use effects on plant diversity extend beyond the boundaries of transformed land by altering habi-
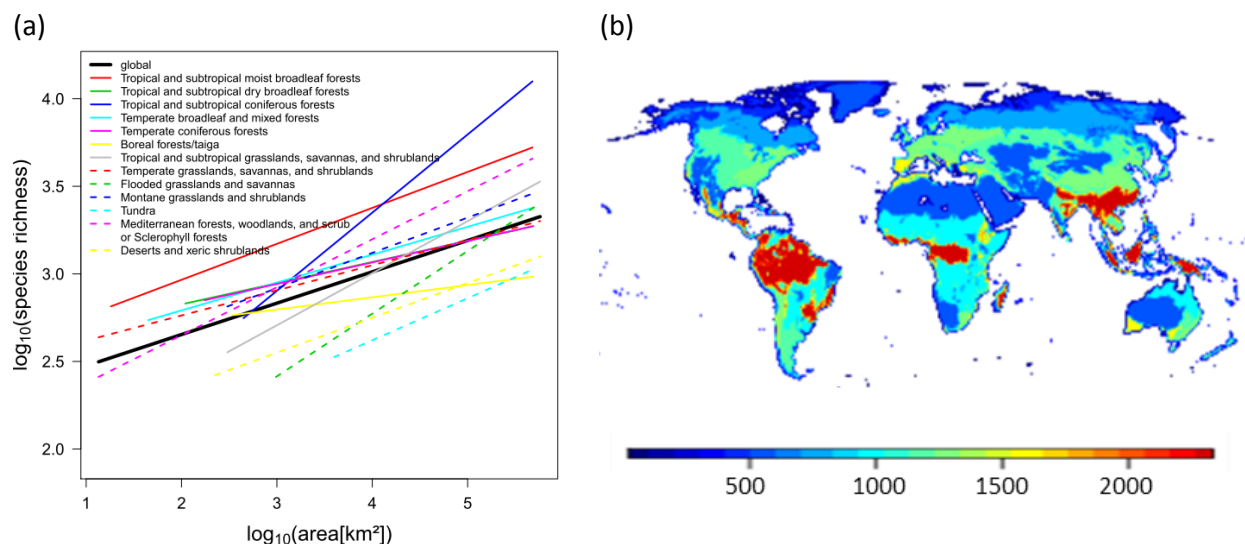
(a)

(b)

Figure 1. (a) Differences in species–area relationship (SAR) curves for vascular plants among biomes. Axes delineate ranges of original data (see Fig. 1b). The lengths of SAR curves reflect the range sizes of sampling units used to fit the relationship. The thick black line indicates the global relationship. **(b)** Predictions of vascular plant species richness for 100 km x 100 km grid cells based on my biome-specific SAR. Figure reproduced with publisher's permission from Gerstner et al. (2014a).

tat characteristics, and thus indirectly affect remaining native vegetation; specific effects might generally depend on the environmental, historical and socio-economic context. Using a meta-analytic framework (sensu Koricheva et al. 2013) and a global dataset extracted from 375 studies, I studied the effects of 11 classes of land use on plant diversity (Fig. 3a). Study designs of the research entering the meta-analysis were very heterogeneous, including both experimental and observational studies, and covered a range in plot sizes of seven orders of magnitude (10^{-2}–10^5 m²). However, we did not find that land-use effects on plant species richness vary systematically with plot size.

The analysis unequivocally demonstrates that land use affects plant species richness, both negatively and positively, but that its effects vary depending on the specific type and location of land use (Gerstner et al. 2014b, Fig. 3b). For example, associations between silviculture and prescribed fire that increase plant species richness have been detected, which can be attributed to mechanisms that directly support species coexistence and persistence (e.g. Tilman 1982). Further, variation of effects was best explained by land-use -specific covariables such as initial land-use system for plantations and abandonment of different

management classes. 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 stronger (Fig. 3c) because more species can be lost in species-rich biomes. This extensive synthesis helps to advance one of the most important debates in the ecological literature – how global biodiversity loss relates to smaller spatial scales and how it is moderated by land use (Bennett 2014).

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

Recent models of environmental change mostly assume that human land use leads to complete habitat loss. This simplistic assumption has been criticized (Pereira et al. 2012, De Camargo & Currie 2015), and species richness patterns in countryside ecosystems, i.e. areas strongly influenced and transformed by humans, are complex (Pereira & Daily 2006, Mendenhall et al. 2014). For example, some species depend on disturbances or open habitats, and colonize human-modified landscapes. SAR approaches that consider the conservation value of such countryside have recently become available (Pereira & Daily 2006), but have been limited to smaller study regions where sam-
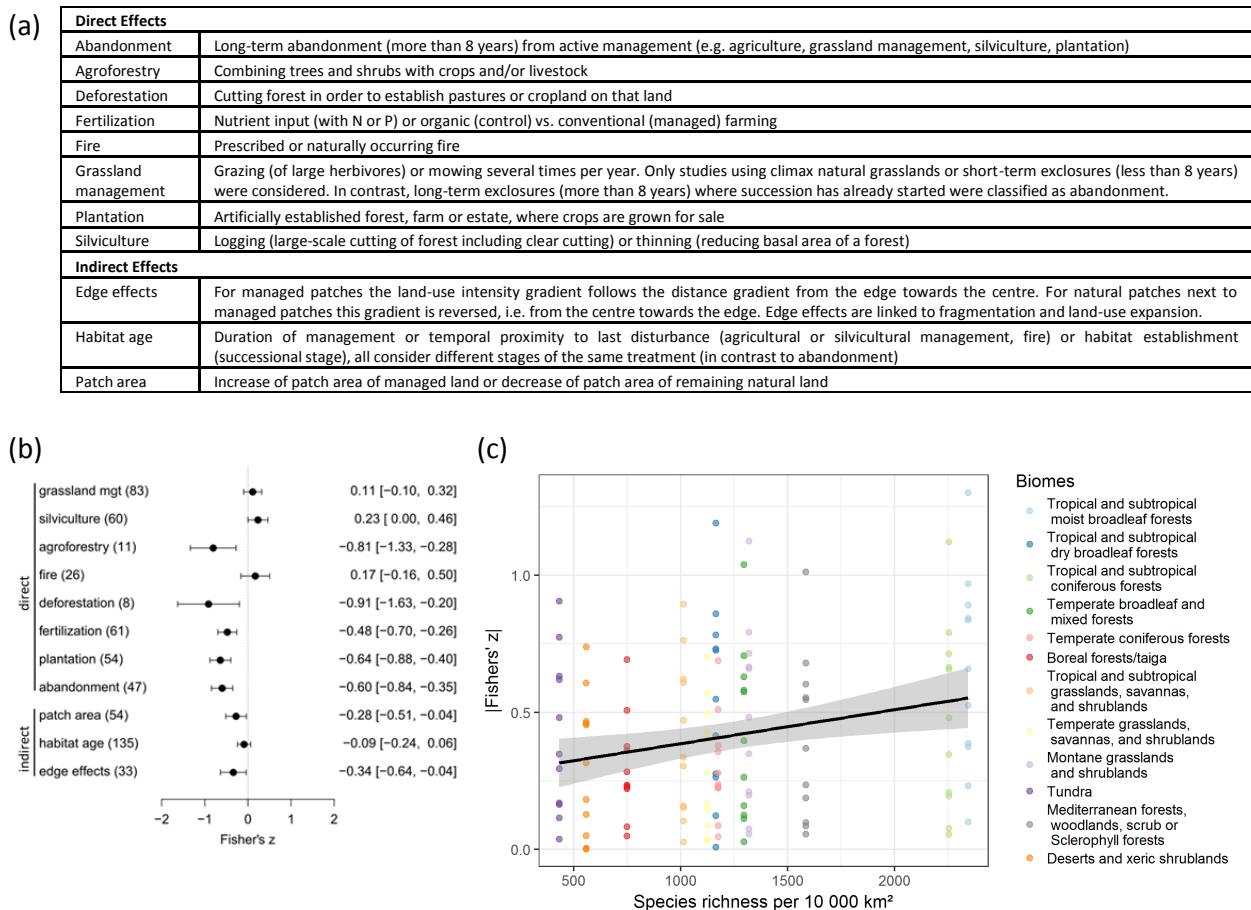
(a)

Direct Effects	
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 Effects	
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, i.e. 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 of patch area of managed land or decrease of patch area of remaining natural land

(b)

(c)

Figure 3. (a) Land-use classes considered and their definitions used in the meta-analysis of Gerstner et al. (2014b). **(b)** 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% confidence interval 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 indicate whether land use is associated with increases or decreases in species richness, respectively. Number of study outcomes is given in brackets. **(c)** Relationship between species pool size, as estimated by the biome-specific SAR per 100 km x 100 km (cf. Fig. 2b), and absolute effect sizes per land-use class in biomes. Species pool size is positively correlated with land-use effects in biomes (r =0.234, P = 0.007). Figures reproduced with publisher's permission from Gerstner et al. (2014b).

pled data or atlas data were available. Such data are scarce at continental scales, so I proposed a new approach to parameterize a countryside SAR and assess the distribution of plant species richness across Europe (Gerstner et al. submitted). I used findings from my previous studies (Gerstner et al. 2014a, Gerstner et al. 2014b) and corrected species pool size at broad grains (50 km x 50 km) and at the same time accounted for local land-use effects (1 km x 1 km).

The countryside SAR accounts for the conservation value of transformed habitat by introducing a parameter h_j reflecting the habitat affinity of a species group to habitat type j, which is the proportion of area that can be effectively used by the species group. I determined the parameter h

using a response ratio (RR), i.e. the ratio between species richness in the modified habitat S_j relative to the species richness of the original habitat S_{orig}, and the slope z of the SAR:

$$h_j = \left(\frac{S_j}{S_{orig}}\right)^{1/z} = RR^{1/z} \qquad (4)$$

A basic formulation of the countryside SAR model is given by:

$$S = c \cdot \left(\sum_i h_j A_j\right)^z \qquad (5)$$

Finally, I combined both models, the biome-specific SAR (eqn. 3) and the basic countryside SAR (eqn. 5) and used the following equation to predict the species richness pattern:

$$\log_{10} S = \sum_i \left(\log_{10} c_i + z_i \log_{10}\left(\sum_j h_{ij}(B_i A)_j\right)\right) \qquad (6)$$

To estimate the habitat affinities of vascular plants to land use h_j (eqn. 3) I used the slopes of the biome-specific SAR curves (Gerstner et al. 2014a) and estimated the response ratios corresponding to land use in Europe using meta-analytical techniques (Gerstner et al. submitted). I analysed a subset of data originally collected for the global meta-analysis (Gerstner et al. 2014b, N=113) that provided means and variances of species richness for different land-use classes and semi-natural, unmanaged vegetation. For the countryside SAR, I considered a number of widespread land uses in Europe which show significant effects on plant species richness in the analysis, i.e. silviculture, plantation/cropland, fertilized land and abandoned land.

Overall, this countryside-SAR approach overcomes the unrealistic assumptions of previous model approaches about constant or generally negative effects of land use (e.g. van Vuuren et al. 2006, Alkemade et al. 2009) and is able to predict species richness changes across spatial scales (in contrast to Newbold et al. 2015). Moreover, such a broad-scale approach allows the study of scenarios of land use and trade-offs with biodiversity resulting from national and international policy changes. Forthcoming studies can help to improve it, e.g. by updating land-use effects on species richness and providing improved maps of land-use indicators. Finally, since climate change results in biome shifts (Hansen et al. 2001), the countryside SAR is able to account for climate change effects in predictions of biodiversity change, by using biome-specific SAR parameters.

Conclusion

Despite limitations and remaining challenges in modelling species richness patterns, my thesis contributes to a deeper understanding of species–area relationships at the macroscale, and of how species richness patterns at broad scales are driven by land use. I have developed a countryside SAR to predict species richness of vascular plants, accounting for land use. Thus, the model overcomes limitations of previous models which have served as a baseline for global assessments (e.g. Millennium Ecosystem Assessment 2005). Moreo-

ver, my countryside SAR model enables predictions about the combined future climate- and land-use-change effects on plant richness, which can be used to better inform environmental policy at the scale of regions to continents. In my thesis I have used vascular plants as the focal taxon, but the approach can be applied to other taxa as well. Furthermore, the approach can be transferred to other regions in which it is feasible to collect such data, and supplemented by integrating effects of other land-use indicators. In the future, appropriate global land-use datasets may become 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).

References

Alkemade, R., van Oorschot, M., Miles, L., Nellemann, C., Bakkenes, M. & ten Brink, B. (2009) GLOBIO3: A framework to investigate options for reducing global terrestrial biodiversity loss. Ecosystems, 12, 374–390.

Arrhenius, O. (1921) Species and area. Journal of Ecology, 9, 95–99.

Barthlott, W., Mutke, J., Rafiqpoor, M.D., Kier, G. & Kreft, H. (2005) Global centres of vascular plant diversity. Nova Acta Leopoldina, 92, 61–83.

Bennett, J. (2014) Editor's Choice: Effects of land use on plant diversity - A global meta-analysis. Journal of Applied Ecology, Editors' Choice 516, http://www.journalofappliedecology.org/view/0/jpeeditorschoice516.html

Brooks, T.M., Mittermeier, R.A., Mittermeier, C.G. et al. (2002) Habitat loss and extinction in the hotspots of biodiversity. Conservation Biology, 16, 909–923.

Cardinale, B.J., Duffy, J.E., Gonzalez, A. et al. (2012) Biodiversity loss and its impact on humanity. Nature, 486, 59–67.

De Camargo, R.X. & Currie, D.J. (2015) An empirical investigation of why species–area relationships overestimate species losses. Ecology, 96, 1253–1263.

Dengler, J. (2009) Which function describes the species–area relationship best? A review and empirical evaluation. Journal of Biogeography, 36, 728–744.

Gerstner, K. (2015) The global distribution of plant species richness in a human-dominated world. PhD thesis, Martin Luther University Halle–Wittenberg. http://digital.bibliothek.uni-halle.de/hs/content/titleinfo/2425240

Gerstner, K., Dormann, C.F., Václavík, T., Kreft, H. & Seppelt, R. (2014a) 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.

Gerstner, K., Dormann, C.F., Stein, A., Manceur, A.M. & Seppelt, R. (2014b) Effects of land use on plant diversity – A global meta-analysis. Journal of Applied Ecology, 51, 1690–1700.

Gerstner, K., Levers, C., Kuemmerle, T., Václavík, T., Pereira, H.M. & Seppelt, R. (submitted) Assessing land-use effects on European plant diversity using a biome-specific countryside species-area model.

Hansen, A.J., Neilson, R.P., Dale, V.H., Flather, C.H., Iverson, L.R., Currie, D.J., Shafer, S., Cook, R. & Bartlein, P.J. (2001) Global change in forests: responses of species, communities, and biomes. BioScience, 51, 765–779.

Harte, J. & Kitzes, J. (2012) The use and misuse of species–area relationships in predicting climate-driven extinction. In: Saving a million species: extinction risk from climate change (ed. by L. Hannah), pp. 73–86. Island Press, Washington, DC.

He, F. & Hubbell, S.P. (2011) Species–area relationships always overestimate extinction rates from habitat loss. Nature, 473, 368–371.

Hooper, D.U., Adair, E.C., Cardinale, B.J., Byrnes, J.E.K., Hungate, B.A., Matulich, K.L., Gonzalez, A., Duffy, J.E., Gamfeldt, L. & O'Connor, M.I. (2012) A global synthesis reveals biodiversity loss as a major driver of ecosystem change. Nature, 486, 105–108.

Isbell, F., Calcagno, V., Hector, A. et al. (2011) High plant diversity is needed to maintain ecosystem services. Nature, 477, 199–202.

Kier, G., Mutke, J., Dinerstein, E., Ricketts, T.H., Küper, W., Kreft, H. & Barthlott, W. (2005) Global patterns of plant diversity and floristic knowledge. Journal of Biogeography, 32, 1107–1116.

Koricheva, J., Gurevitch, J. & Mengersen, K. (2013). Handbook of meta-analysis in ecology and evolution. Princeton University Press, Princeton, New Jersey, USA.

Kreft, H. & Jetz, W. (2007) Global patterns and determinants of vascular plant diversity. Proceedings of the National Academy of Sciences USA, 104, 5925–5930.

Ladle, R.J. & Whittaker, R.J. (eds)(2011) Conservation biogeography. Wiley–Blackwell, Chichester, UK.

Lambin, E.F. & Meyfroidt, P. (2011) Global land use change, economic globalization, and the looming land scarcity. Proceedings of the National Academy of Sciences USA, 108, 3465–3472.

Mendenhall, C.D., Karp, D.S., Meyer, C.F.J., Hadly, E.A. & Daily, G.C. (2014) Predicting biodiversity change and averting collapse in agricultural landscapes. Nature, 509, 213–217.

Millennium Ecosystem Assessment (2005) Ecosystems and human well-being: synthesis. Island Press, Washington DC.

Newbold, T., Hudson, L.N., Hill, S.L. et al. (2015) Global effects of land use on local terrestrial biodiversity. Nature, 520, 45–50.

Pereira, H.M., Borda-de-Água, L. & Martins, I.S. (2012) Geometry and scale in species–area relationships. Nature, 482, E3–E4.

Pereira, H.M. & Daily, G.C. (2006) Modeling biodiversity dynamics in countryside landscapes. Ecology, 87, 1877–1885.

Pimm, S., Russell, G., Gittleman, J. & Brooks, T. (1995) The future of biodiversity. Science, 269, 347–350.

Rosenzweig, M.L. (1995) Species diversity in space and time. Cambridge University Press, Cambridge, UK.

Storch, D., Marquet, P.A. & Brown, J.H. (2007) Scaling biodiversity. Cambridge University Press, Cambridge, UK.

Tilman, D. (1982) Resource competition and community structure. Monographs in Population Biology Series. Princeton University Press, Princeton, New Jersey, USA.

Thomas, C.D., Cameron, A., Green, R.E. et al. (2004) Extinction risk from climate change. Nature, 427, 145–148.

Turner, B.L., Lambin, E.F. & Reenberg, A. (2007) The emergence of land change science for global environmental change and sustainability. Proceedings of the National Academy of Sciences USA, 104, 20666–20671.

Turner, W.R. & Tjørve, E. (2005) Scale-dependence in species–area relationships. Ecography, 28, 721–730.

van Vuuren, D.P., Sala, O.E. & Pereira, H.M. (2006) The future of vascular plant diversity under four global scenarios. Ecology and Society, 11, 25.

Verburg, P.H., Erb, K.-H., Mertz, O. & Espindola, G. (2013) Land system science: between global challenges and local realities. Current Opinion in Environmental Sustainability, 5, 433–437.

Whittaker, R.J. & Matthews, T.J. (2014) The varied form of species–area relationships. Journal of Biogeography, 41, 209–210.