Understanding species responses to habitat change across scales using the countryside species-area relationship

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To my grandmother Maria

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Summary

Land use change is an undisputed major driver of biodiversity change, affecting species richness patterns from local to global scales. Yet, current assessments of biodiversity change frequently neglect that species often face habitat change instead of habitat loss, and that not all species respond equally to it. Understanding how humans contribute to biodiversity changes (past and present), is essential to improve our capacity to assess and predict how different socioeconomic choices affect biodiversity.

The overall aim of this dissertation was to improve existing methods that enable a more accurate assessment of local, regional and global biodiversity change as a result of habitat change, and demonstrate the applicability of such methods in relevant case studies. The countryside Species-Area Relationship (cSAR) model has been explored, because of its unique capacity to predict biodiversity change after habitat conversion, to study the range and intensity of species responses to land use change, and to describe the use of human-modified landscapes by different functional species groups (i.e., here defined as species groups composed by species with similar habitat preferences).

In the first study (**Chapter 2**), I assess the added value of land use related variables to current modelling frameworks when assessing species richness patterns at large scales, as well the relationship between species richness and habitat heterogeneity. The analysis shown that integrating varying land use effects into a SAR model leads to considerable improvement of the prediction of species richness patterns at larger scales, findings that align with previous local scale research. The assumption that the modified landscape is completely inhospitable is undoubtedly overly simplistic. By considering the differential use of habitat by different species groups, the countryside SAR model gives a much more holistic picture than the classic SAR model.

In most real-world situations, the likelihood of species undergoing extinction following habitat loss will depend on their sensitivity to the modified habitat and the capacity of the modified habitats to support them. In the second study (**Chapter 3**), I first examined the global distribution of species responses to full habitat conversion into different human-modified habitats. This analysis shows that species response to habitat conversion vary significantly between land-use types, with some studies even reporting a positive response to human-modified habitats. I then explored how to scale the results from such studies from the local scale to the larger scales at which researchers often want to make projections of biodiversity change. This analysis shows that these studies cannot be linearly scaled from plots to large regions, at risk of overestimating the proportion of species going

extinct. Hence, how species perceive the landscape and are impacted by habitat conversion is a scale-dependent phenomenon. When modeling biodiversity responses to habitat conversion, one has to consider that the impacts of land use change on biodiversity at a larger scale and within the context of heterogeneous landscapes may be different than plot-scale effects. Here, the countryside SAR model, as a modification of the classic SAR model, provides an unifying framework to account both for the effects of species persistence on the matrix and for the non-linear relationship between habitat area and species richness.

In the third and fourth studies (**Chapter 4 and 5**) of this dissertation the application of the countryside SAR is demonstrated in particular case studies, which not only serve as a vehicle to illustrate the methods, but also provide findings relevant for addressing global environmental challenges. For instance, the third study provides a comprehensive and systematic assessment of the global impacts of 14 agricultural and forestry activities (i.e., socioeconomic activities) on biodiversity and carbon sequestration, taking complex production-consumption interlinkages into account. The countryside SAR framework is used to link resource consumption and biodiversity change while explicitly considering species affinity to specific land use sectors. Here particular drivers of biodiversity and carbon sequestration losses are identified in different regions of the world, which can inform the consuming nations of their environmental footprint domestically and abroad.

In the fourth study, I then assessed how future socioeconomic developments may affect biodiversity, by performing a scenario analysis of alternative plausible futures. While, it is unavoidable that future socioeconomic developments will lead to further biodiversity change, different choices can impact species differently. Therefore, assessing the impact of such developments on different species communities (e.g., specialists *versus* generalists) will help anticipate changes and guide conservation actions. In the fourth study, I address this research priority using Portugal as a case study. This scenario analysis illustrates how future biodiversity impacts can differ depending upon the intervention plan and the regional social-economic context. Results from the countryside SAR model allowed us to pinpoint how different socioeconomic developments may affect local species communities, by identifying which species functional groups are likely to be the winners or losers of such developments.

Overall, this dissertation expands our understanding of species responses to habitat change, while refining a tool to predict biodiversity change across scales, allowing for more accurate detailed and multi-scale assessments and predictions of species responses to habitat change and degradation.

Chapter 1

Introduction

1.1 Habitat change and biodiversity decline

Humans have reshaped our planet for millions of years (Turner and McCandless 2004). Firstly, through the use of fire and hunting, gathering and fishing; then through the domestication of animals and plants, and more recently through the use of fossil-fuels (Pereira *et al.* 2012a). After the industrial revolution, land use activities accelerated, with the area used for crops and pasturelands expanding fivefold. Cropland expansion occurred mostly in forested areas, while pastureland expansion replaced mostly grasslands, savannas and shrublands (Ramankutty *et al.* 2018). By 2000, agricultural expansion alone was responsible for converting about 30% of forests worldwide (Ramankutty *et al.* 2008), and close to 80% of all ice-free land on Earth was reportedly affected by either land management or land conversion (Ellis *et al.* 2010). These conversions make land use not only a major force driving global environmental change, but also the current primary driver of biodiversity and ecosystems change (Leadley *et al.* 2010; Pereira *et al.* 2012a).

Biodiversity has been declining steadily over the last decades (Butchart *et al.* 2010; Pimm *et al.* 2014). While biodiversity loss has multiple drivers, such as climate change, invasive species, overexploitation, and pollution (IUCN 2017), the International Union for Conservation of Nature (IUCN) Red List of Threatened Species identifies habitat change and habitat degradation as the main current threats to plants and vertebrates, affecting more than 80% of globally threatened mammals, birds, and amphibians. (Pereira *et al.* 2012a). Habitat change directly affects biodiversity by reducing or modifying the habitat available to species.

In the future, both human population and per capita wealth are projected to increase (van Vuuren *et al.* 2012), leading to further pressures on land use. For instance, food consumption is expected to increase by 1.7 times by 2050, while wood consumption is expected to increase by 1.3 times (Alexandratos and Bruinsma 2012; van Vuuren *et al.* 2012). Given the historical changes observed, such increase in consumption is likely to lead to further land-use demand and other environmental changes, causing additional biodiversity loss. International agreements such as the United Nations Sustainable Development Goals (SDGs; UN General Assembly 2015) and the Convention on Biological Diversity Aichi targets (CBD 2010) commit to reducing these losses.

The Intergovernmental Platform on Biodiversity and Ecosystem Services (IPBES) has identified that reporting past, present and future trends of biodiversity at global and regional levels and development of scenarios is key to help decision makers evaluate different policy options (Ferrier *et al.* 2016). With habitat change being a dominant driver of global biodiversity change (Leadley *et al.* 2010; Pereira *et al.* 2010) its incorporation into modelling approaches is of major importance for current and future scenario analyses and conservation planning. However, the impacts of habitat change are complex and difficult to quantify.

This dissertation expands our understanding of species responses to habitat change, while refining a tool to predict biodiversity change across scales, allowing for more accurate assessments and predictions of species responses to habitat change and degradation.

1.2 Response of biodiversity to habitat change

Although rapid habitat change can occur naturally (e.g., droughts, fire, hurricanes), it is generally induced by human activities. Habitat change can be characterized by the conversion of natural habitat to human-modified habitat, by the intensification of human activities in already modified habitats, or by the recovery of natural vegetation and forest after human activities cease (Pereira *et al.* 2012a). Current assessments of biodiversity change frequently neglect that species often face habitat change instead of habitat loss, and that not all species respond equally to habitat change (Chaudhary *et al.* 2015; Titeux *et al.* 2016). For instance, the effects of land use may vary depending on what is perceived as real habitat by different species (Pereira & Daily (2006) and see Chapter 3). Furthermore, the impact of land use change on species will not only depend on the amount of land used, but also on the spatial patterns as well as the way in which the land is used (i.e., the intensity and type of land-use) by the different species (Tews *et al.* 2004; Chaudhary *et al.* 2015). While some species may decrease in abundance or even go extinct when habitat change occurs, other species may remain unaffected or even thrive under the new conditions (Desrochers *et al.* 2011; Newbold *et al.* 2015). Therefore, there is a growing recognition that although the conversion of native habitat to human-modified habitats is followed by biodiversity loss, human-modified landscapes can also support significant levels of biodiversity, particularly when key structures remain (Pereira and Daily 2006; Koh and Ghazoul 2010; Mendenhall *et al.* 2014; Chaudhary *et al.* 2015). Thus, it is essential that we improve existing methodologies to account for habitat preferences when assessing and predicting biodiversity change across scales.

1.3 Modelling biodiversity responses to habitat change

1.3.1 Species-Area Relationship models

The Species-Area Relationship (SAR) is one of the oldest known patterns in ecology and has been studied for decades in a wide variety of systems and scales (e.g., Preston, 1960; Connor & McCoy, 1979; Rosenzweig, 1995). First observed by (Watson 1835), the SAR represent species richness explicitly as a function of sampling area. Classically, SARs have been drawn by sampling different sized areas, which may be nested (e.g., each smaller area is completely contained within the next area, larger than the previous) or non-overlapping isolates samples (e.g., series of islands or discrete forest patches). In nested SARs, species must be at least monotonically increasing or monotonically non-decreasing with area size, while in isolate SARs species numbers may increase or decrease with area size, given that a larger unit may not necessary have more species than smaller ones (Rosenzweig 1995; Scheiner *et al.* 2011; Pereira and Borda-de-Água 2013). A great deal of discussion has focused on the properties of SARs composed in these different ways (Rosenzweig 1995; Dengler and Oldeland 2010; Scheiner *et al.* 2011). In this dissertation, only the proprieties of nested SARs are discussed.

The shape this relationship takes has also been debated extensively (Triantis *et al.* 2012; Matthews *et al.* 2015), and is known to be influenced by geographical and evolutionary factors (Franzén *et al*., 2012) , ecological processes (Drakare *et al.* 2006; Matias *et al.* 2014; With 2016), and scale (Hubbell 2001; Rosenzweig 2001; Scheiner *et al.* 2011). Consequently, many functions for fitting the SAR have been proposed through the years, both based on field studies or simulations (e.g., Scheiner, 2003; Tjørve, 2003; Tjørve & Tjørve, 2008; Scheiner *et al*., 2011; Triantis *et al*., 2012). Among these functions, the power model, $S = cA^z$ (where S is the number of species in area A, and c and z are the fitted parameters), proposed by Arrhenius (1921), remains the most frequently preferred model (Figure 1.1). The power model has been shown to describe SARs appropriately under most conditions (e.g., Connor and McCoy 1979; Lomolino 2000; Dengler 2009; Triantis *et al.* 2012; He and Hubbell 2013), and even proposed as an universal model (Dengler 2009). Furthermore, the parameters of the power SAR have ecological interpretations. The constant c describes the number of species in one unit of area, whereas the constant z is the rate of change in the number of species with increasing area (Tjørve and Tjørve 2008).

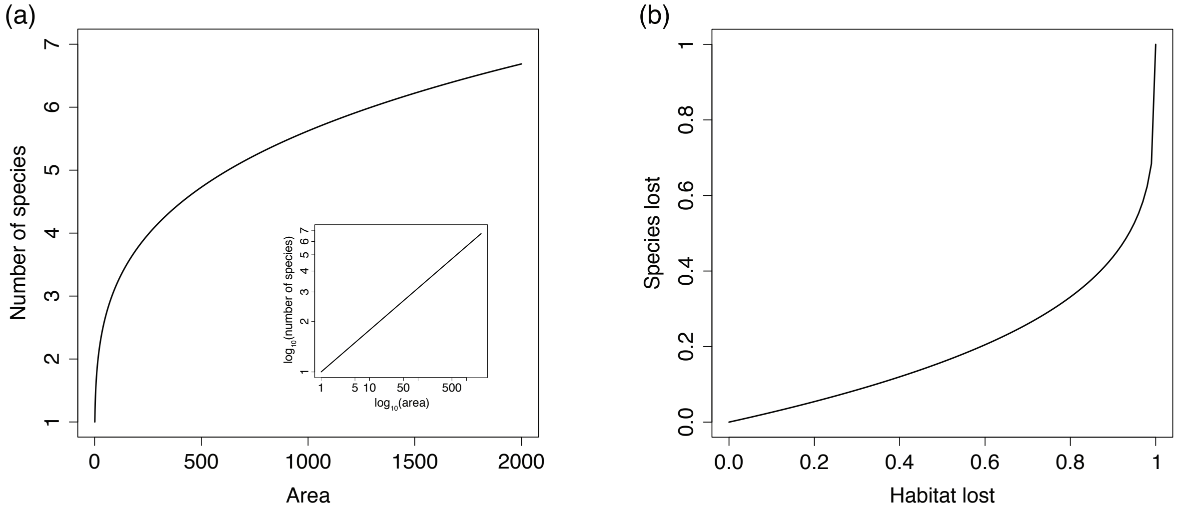

Figure 1.1. How the Species-Area Relationship (SAR) can be used to predict species loss. (a) Representation of a nested species-area relationship modeled by a power law in arithmetic space and in log-log space (inset figure). (b) Predicted fraction of species lost as a function of the fraction of habitat lost (obtained by following along the nested SAR from (a) as area decreases).

Species-Area Relationship (SAR) models have been widely used to compare species diversity patterns when regions differ in area, predict the response of species richness to habitat area loss and estimate species extinctions (Pimm and Askins 1995; van Vuuren *et al.* 2006). Despite being applied in a number of studies, the use of the standard SAR is still controversial, particularly since SARs are based on several simple assumptions which might not be met in reality (e.g., Dial & Budiansky, 1994; Heywood et al., 1994; Pimm & Askins, 1995; Brooks & Balmford, 1996; Thomas et al., 2004). Recently, several studies have discussed whether SARs are an appropriate method to estimate species loss due to habitat loss (i.e., species extinctions), as predicted extinctions based on this method and recorded extinctions often do not agree (He and Hubbell 2011; Rahbek and Colwell 2011; Pereira *et al.* 2012b; Thomas and Williamson 2012). This debate has generated several valuable insights, such as the role of aggregation of individuals (He and Hubbell 2013), the importance of the ecological context (Rybicki *et al.* 2013; Matias *et al.* 2014) and the influence of scale and geometry of habitat loss (Pereira *et al.* 2012b; Keil *et al.* 2015). However, this debate has not yet been settled, and there are still critical unresolved issues. One critical issue is the assumption of the classic SAR that no species persist outside native habitats, and that when all habitat is converted to human-modified habitats (e.g., agricultural lands) all species go extinct. In reality many species are able to persist in human-modified habitats (see section 1.2). For instance, the IUCN reports that at least 47% of extant bird species use human-modified landscapes, with 32% using agricultural habitats specifically (IUCN 2017). Moreover, related variables such as habitat heterogeneity are seldom considered in modelling approaches at larger scales. Another issue is that the classic SAR framework ignores functional differences among species and thus considers all species as ecologically equivalent. Finally, spatial scale is a fundamental, but still mostly overlooked, aspect of understanding species responses to habitat change. Throughout the different chapters of this dissertation, I explore and discuss these issues in detail using an alternative and improved SAR framework that explicitly overcomes these limitations of the classic approach (see section 1.3.2).

1.3.2 Multi-habitat Species-Area Relationship models

Although scientists have long recognized the importance of the habitat in determining species richness, until recently, only the area of available pristine habitat has been considered in SAR models. The absence of a simple and easily usable mathematical model connecting species richness and habitat variables have prevented the widespread use of habitat characteristics. In the last decade and a half, a number of SAR-based models have been put forward that considered both habitat area and habitat composition (i.e., number and types of habitats) to explain species richness patterns (hereafter called multi-habitat SAR models). For instance, Tjørve (2002) proposed a framework to build species diversity models in multihabitat landscapes by combining species-area curves for different habitats. The main idea is to subtract the number of species overlapping between two habitats from the total number of species found in the different habitats. In Tjørve (2002) model, the effect of the number of habitats and their sizes are the only factors considered. To date, this model has yet to be tested or empirically compared with other models.

A year later, Triantis *et al*. (2003) proposed the choros model as a way of accounting for the number of different habitat types in the classic SAR. The choros model combines the total effects of area and habitat diversity to determine the regional species richness. The variable ‘area’ is replaced by the variable ‘choros’ (*K)*, which arises as the result of the multiplication of the number of different habitats in an area (*H*) by the size of that area (*A*), $K = H.A$. The species richness of a region is then expressed as a power function of the choros *K*. In contrast to Tjørve (2002), the Triantis *et al*. (2003) model has been shown to outperform the classic SAR (Triantis *et al.* 2003; Proença and Pereira 2013). More recently, Koh and Ghazoul (2010) highlighted the importance of considering the specific responses of taxa to the area of habitats and to the quality of the surrounding matrix. Koh and Ghazoul (2010) proposed the matrix-calibrated SAR, where matrix effects are incorporated in the SAR framework by partitioning the *z*-value of the power model into two components: *y*, a constant that describes the complete unsuitabilily of the matrix to the analysed taxa, and σ, a measure of sensitivity of a specific taxon to the full conversion of native habitat into the modified habitat. In contrast to the previous models, this model considers the possibility of differential use of habitats by different taxon and has also shown to outperform the classic SAR. However, another multi-habitat SAR model has been shown to outperform both the choros model and the matrix-calibrated SAR model (Pereira *et al.* 2014), as well as the classic SAR, in explaining species richness patterns in multihabitat landscapes: the countryside SAR model (Pereira and Daily 2006).

Proposed by Pereira and Daily (2006), the countryside SAR (cSAR) model was the first model to describe the use of both human-modified and native habitats by different species. The countryside SAR accounts for the differential use of habitats by different functional species groups (i.e., species groups composed by species with similar habitat preferences) by introducing a parameter h_{ij} reflecting the habitat affinity of a species group *i* to an habitat type *j*. This parameter can be seen as the proportion of area of an habitat type *j* that can be effectively used by a species group *i*, and can be related to the measure of sensitivity σ described by Koh and Ghazoul (2010) as shown by Pereira et al. (2014) (see Chapter 3). The countryside SAR builds on the classic SAR and its application requires two steps. First, the countryside SAR estimates the species richness of groups composed by species with similar habitat preferences, Eq. 1, where S_i is the number of species in group *i*, *n* is the number of modified habitat types and A_j is the area covered by habitat *j*:

$$S_i = c_i \left(\sum_{j=1}^{n} h_{ij} A_j \right)^z . \tag{1}$$

Then, the total number of species in the landscape, S_i, is given by the sum of species in each group (Eq. 2), where *m* is the number of species groups:

$$S = \sum_{i=1}^{m} S_i . \tag{2}$$

After habitat conversion, the proportion of species remaining in the landscape will depend on the level of affinity of the species group to the human-modified habitats. This model has been successfully applied to estimate species richness within human-modified landscapes (Guilherme and Pereira 2013; Proença and Pereira 2013; Gerstner *et al.* 2017) and quantify the impacts of land use change (Pereira *et al.* 2014; Chaudhary *et al.* 2015; Chaudhary 2016; Chaudhary and Brooks 2017).

Despite the significant advances made towards assessing land use impacts on biodiversity using the countryside SAR model, several research gaps and scope for improvement remain. For instance, previous works have successfully applied the countryside SAR to model species richness patterns of birds (Guilherme and Pereira 2013) and plants (Proença and Pereira 2013) at the local scale. To date, however, it is unknown if the countryside SAR model is able to describe the use of human-modified landscapes by different species groups at larger scales. Recent assessments at larger scales (Chaudhary *et al.* 2015; Gerstner *et al.* 2017; Chaudhary and Brooks 2017) have neglected the differential use of habitats by different species groups and have uniquely focused on different taxonomic groups (e.g., birds, mammals, plants).

1.4 Objectives of the dissertation

Understanding how humans contribute to biodiversity changes (past and present), is essential to improve our capacity to assess and predict how different socioeconomic choices affect biodiversity. Only with this knowledge can we hope to combine human development and nature stewardship in a sustainable way (Rosa *et al.* 2017).

The overall aim of this dissertation was, therefore, to improve existing methods that enable a more accurate assessment of local, regional and global biodiversity change as a result of habitat change, and demonstrate the applicability of such methods in relevant case studies. In particular, I studied the impact and influence that different types of human-modified habitats , and their area, have in the distribution and richness of species across the landscape and across scales. The countryside SAR model has been explored, because of its unique capacity to predict biodiversity change after habitat conversion (see Chapter 3 and Chapter 4), to study the range and intensity of species responses to land use change (see Chapter 2 and Chapter 3) and to describe the use of human-modified landscapes by different functional species groups (see Chapter 2 and Chapter 5). This dissertation is organized as follows:

In **Chapter 2,** I investigated the added value of incorporating land use related variables into models with well-accepted predictors, namely climate, topography and area, when explaining species richness patterns at the regional scale (Iberian Peninsula). More specifically, I analyzed the relationship between habitat heterogeneity and species richness of amphibians, reptiles and passerines at two different spatial resolutions in the Iberian Peninsula. I subsequently assessed the individual and joint effects of different climatic, topographical and habitat variables when explaining species richness patterns. Finally, I investigated the contribution of land use variables to species-area models by comparing the fit of the countryside SAR model with the fit of the classic SAR model. The chapter thus demonstrates how land use related variables can add relevant information to current modelling frameworks when assessing species richness patterns at large scales. Furthermore, the countryside SAR parameters estimated in this chapter are relevant for **Chapter 5**.

The work of **Chapter 2** was published as: Martins I.S., Proença V., & Pereira H.M. (2014) The unusual suspect: Land use is a key predictor of biodiversity patterns in the Iberian Peninsula. *Acta Oecologica*, 61, 41–50. doi: 10.1016/j.actao.2014.10.005.

Chapter 3 examines the distribution of species responses to full habitat conversion into different human-modified habitats, using studies collected worldwide. This data was then used to estimate habitat affinities for the countryside SAR model (see section 1.3.2). I then explored how to scale the response of biodiversity to land use change from the local scale (i.e., the scale of the studies collected) to the larger scales at which researchers often want to make projections of biodiversity change. Finally, in this Chapter I discussed how the countryside SAR provides a framework to project short-term species extinctions that take into account species persistence in the landscape matrix and the non-linearity of the response of biodiversity to land use change across sampling scales.

The work presented in **Chapter 3** was published as: Martins, I.S. & Pereira, H.M. (2017) Improving extinction projections across scales and habitats using the countryside species-area relationship. *Scientific Reports*, 7, 12899.

In **Chapter 4**, we provide a temporal assessment of the global impacts of 14 agricultural and forestry activities (i.e., socioeconomic activities) on biodiversity and carbon sequestration based on the most recent available data, combined with biophysical and economic models. In particularly, we explored how the countryside SAR framework can be used to link resource consumption and biodiversity change while explicitly considering species affinity to specific land use sectors (**Chapter 3**). Finally, teleconnections between world regions (through international trade) and the production-consumption interlinkages were discussed. The work presented in **Chapter 4** is currently to be resubmitted to *Nature Ecology and Evolution* after undergoing major revisions based on the feedback received from the reviewers after an initial submission *to Nature*.

Chapter 5 assesses how future socioeconomic developments may affect biodiversity, by performing a scenario analysis of alternative plausible futures. Using Portugal as a case study, this chapter uses the countryside SAR model and the habitat affinities calculated in **Chapter 2**, to assess how biodiversity will respond to three distinct land use change scenarios, and how different functional species groups will perceive the habitat changes projected in each scenario. I compared species responses, between and within three species groups (i.e., forest species, farmland species and species with affinity for other natural habitats), to the alternative future human-modified landscapes and discussed the differences and similarities. The work presented in this chapter is currently in preparation for submission to Landscape Ecology.

Chapter 6 summarizes the findings of the entire dissertation and provides scientific and practical relevance of the results. It further discusses remaining challenges and limitations, and suggests future research to improve assessments of biodiversity responses to habitat change and degradation across spatial scales.

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Chapter 2

The unusual suspect: Land use is a key predictor of biodiversity patterns in the Iberian Peninsula

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Original article

The unusual suspect: Land use is a key predictor of biodiversity patterns in the Iberian Peninsula

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ABSTRACT

Although land use change is a key driver of biodiversity change, related variables such as habitat area and habitat heterogeneity are seldom considered in modeling approaches at larger extents. To address this knowledge gap we tested the contribution of land use related variables to models describing richness patterns of amphibians, reptiles and passerines in the Iberian Peninsula. We analyzed the relationship between species richness and habitat heterogeneity at two spatial resolutions (i.e., 10 km × 10 km and 50 km × 50 km). Using both ordinary least square and simultaneous autoregressive models, we assessed the relative importance of land use variables, climate variables and topographic variables. We also compare the species–area relationship with a multi-habitat model, the countryside species–area relationship, to assess the role of the area of different types of habitats on species diversity across scales. The association between habitat heterogeneity and species richness varied with the taxa and spatial resolution. A positive relationship was detected for all taxa at a grain size of 10 km × 10 km, but only passerines responded at a grain size of 50 km × 50 km. Species richness patterns were well described by abiotic predictors, but habitat predictors also explained a considerable portion of the variation. Moreover, species richness patterns were better described by a multi-habitat species-area model, incorporating land use variables, than by the classic power model, which only includes area as the single explanatory variable. Our results suggest that the role of land use in shaping species richness patterns goes beyond the local scale and persists at larger spatial scales. These findings call for the need of integrating land use variables in models designed to assess species richness response to large scale environmental changes.

1. Introduction

Explaining the spatial patterns of species richness is a central goal in ecology (Rosenzweig, 1995). Several explanatory factors have been identified, including energy availability, habitat heterogeneity, area, evolutionary history, and geometric constraints, that is, physiographical and physiological boundaries (Rahbek and Graves, 2001).

Land use change has a direct effect on some of these factors, namely on habitat heterogeneity and area, and was the main direct driver of biodiversity loss and change in terrestrial systems at regional and global scales during the past century (Pereira et al., 2012). While the role of land use in shaping species richness patterns at local scales is well described (Atauri and de Lucio, 2001; Tews et al., 2004), there is still a knowledge gap regarding its effect at regional and global scales.

On the other hand, climate is often reported as the main predictor of species richness at large spatial extents (Hawkins et al., 2003; Field et al., 2009). Climate affects species richness, from variations in productivity to establishing physiological limits (Clarke and Gaston, 2006). However, given current and predicted rates of land use change, modeling approaches largely based on climate will be limited in their predictive power (Thuiller et al., 2004). For example, species that are highly sensitive to habitat change and degradation may be absent from areas with potentially suitable climate conditions. In addition, it has been reported that the interacting effects of climate change and land use change may

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have a greater impact on biodiversity than their individual effects (Clavero et al., 2011; Mantyka-pringle et al., 2012).

In addition to the relative effect of land use and climate on species richness patterns, there is an ongoing debate about the concurrent role of habitat composition or heterogeneity (i.e., number of habitats in an area) and habitat area, both land use related variables, in determining species richness in a particular region or scale (MacArthur and Wilson, 1967; Rosenzweig, 1995; Tjørve, 2002; Tews et al., 2004; Desrochers et al., 2011). However, disentangling the individual effect of each factor is not straightforward because the two factors tend to be correlated, that is, larger spatial areas also tend to encompass a larger number of habitats (Ricklefs and Lovette, 1999; Triantis et al., 2003; Desrochers et al., 2011).

The response of species richness to habitat area loss is often assessed using species—area relationship (SAR) models (Arrhenius, 1921; Brown and Lomolino, 1998). The classic SAR or power model (Arrhenius, 1921) assumes that the number of species is mainly determined by habitat area, and that the habitat is uniform and continuous. Hence, when using the classic SAR, only the responses to changes in habitat area are captured, leaving out the responses to changes in habitat composition. This is particularly relevant in those situations where land use change causes habitat modification instead of real habitat loss (Guilherme and Pereira, 2013; Proença and Pereira, 2013). A possible approach to this issue is the use of multi-habitat SARs (Tjørve, 2002; Triantis et al., 2003; Pereira and Daily, 2006; Koh and Ghazoul, 2010).

Moreover, though area and habitat heterogeneity tend to be positively correlated, their combined effect on species richness may generate a unimodal relationship between species richness and habitat heterogeneity, due to a trade-off between species pool size and the probability of stochastic extinctions of species with low population sizes (Allouche et al., 2012), or in other words, between average habitat size and population size. Therefore, the shape of the relationship will vary depending on the niche width of species in the community, that is, specialist species (narrower niche) will be more affected by declining habitat size as habitat number increases than generalist species (wider niche). Still, more research is needed regarding the shape of this relationship, and in particular, there is still a lack of studies that consider multiple spatial scales and taxa (Tews et al., 2004).

Finally, the relative importance of explanatory factors in shaping species richness patterns may vary with the scale of analysis (Rahbek and Graves, 2001; Willis and Whittaker, 2002; Luoto et al., 2007; Hortal et al., 2008). Therefore, when modeling species richness distribution the choice of spatial scale (i.e., grain size or resolution and extent of the data or overall size of the study area) can directly affect results and limit their comparison with similar studies (Rahbek, 2005).

Here, we examine the relationship between land use related variables, and the species richness distribution of terrestrial vertebrates in the Iberian Peninsula. We investigate the added value of land use variables to models incorporating well accepted predictors, namely climate, topography and area, when explaining species richness patterns. We start by testing the association between habitat heterogeneity and species richness of amphibians, reptiles and passerines, at two different spatial resolutions (i.e., 10 km × 10 km and 50 km × 50 km). We then analyze the individual effects of sets of climate, topography, and habitat variables on the richness of these taxa, and proceed to explore their joint effects using a multimodel approach, at a spatial resolution of 10 km × 10 km. Finally, we investigate the contribution of land use variables to species-area models, by comparing the fit of the countryside SAR model that considers species affinity to different land uses, with the fit of the classic SAR model. We predict that species richness will show a unimodal response to habitat heterogeneity as predicted by the area-heterogeneity trade-off hypothesis (Allouche et al., 2012) at 10 km × 10 km resolution, but also that this pattern will be less perceptible at the 50 km × 50 km resolution, due to weaker area effects on population size. Moreover, we hypothesize that land use related variables play a role in shaping species richness patterns beyond local scales.

2. Methods

2.1. Study area

We selected the Iberian Peninsula as the study area. The environmental context of the Iberian Peninsula, between two biogeographic regions (the Mediterranean and the Atlantic) and featuring several mountain chains, grants this region a high diversity of habitats and species communities. The Mediterranean region encompasses almost the entire surface of Spain and Portugal and is characterized by warm to hot, dry summers with a lengthy period of drought. The Atlantic region includes the north and northwest coastland of the peninsula, and is characterized by cold winters and lack of a distinct dry season. The elevation ranges from sea level to 3478 m, and the mean annual air temperature ranges from below 2.5 °C in areas at highest altitude, namely in the Pyrenees, to temperatures higher than 17 °C in southeast Spain. Mean annual precipitation shows a large spatial variability, with the highest values above 2200 mm and usually in mountain areas, and the lowest values being below 300 mm in the southeast of Spain (AEMet and IM, 2011).

2.2. Data sources

We retrieved species distribution data in 10 km × 10 km UTM cells in the Iberian Peninsula from published atlases for 182 vertebrate species (Fig. 1): 87 passerines (Martí and del Moral, 2003; Equipa Atlas, 2008), 64 reptiles and 31 amphibians (Pleguezuelos et al., 2002; Loureiro et al., 2008). These taxa were selected due to the availability of high quality data on their distribution at the Iberian scale. We excluded marine and aquatic species.

We merged two land cover datasets (Fig. 2, for more detail see Table A.1 in Supplementary Information): the Portuguese land cover map, COS'90 (IGP, 1990), and the land cover map of the Second Spanish National Forest Inventory, IFN2 (MARM, 1998). Water bodies, rocky areas, human-dominated areas (e.g. urban fabric, quarries, green urban areas, etc.) and unclassified land cover were excluded from both datasets. We intersected the land cover maps with the 10 km × 10 km UTM grid and selected grid cells with at least 25% cover, resulting in a final set of 5885 cells. The percentage cover of each habitat in each cell was calculated using ArcGIS 9.3 (ESRI, 2009). We derived climatic variables from the WorldClim dataset on a 1 km resolution (Hijmans et al., 2005), and collected topographic data from the United States Geological Survey HYDRO 1 km digital terrain model for Europe (USGS, 2000). Slope inclination and aspect variables were combined in a Radiation Index ($RI = f(\text{aspect} + \text{inclination} + \text{latitude})$; Oke, 1987). We then aggregated these variables in a 10 km × 10 km UTM grid using ArcGIS 9.3 (ESRI, 2009), to match the resolution of species and land cover data.

To avoid multicollinearity between the independent variables, we performed pairwise correlations tests using the Spearman's rank correlation coefficient. Variables strongly correlated (i.e., $rho > 0.7$) were identified and the variables explaining less variance overall were removed from the analysis (Elith et al., 2006; Wisz and Guisan, 2009).

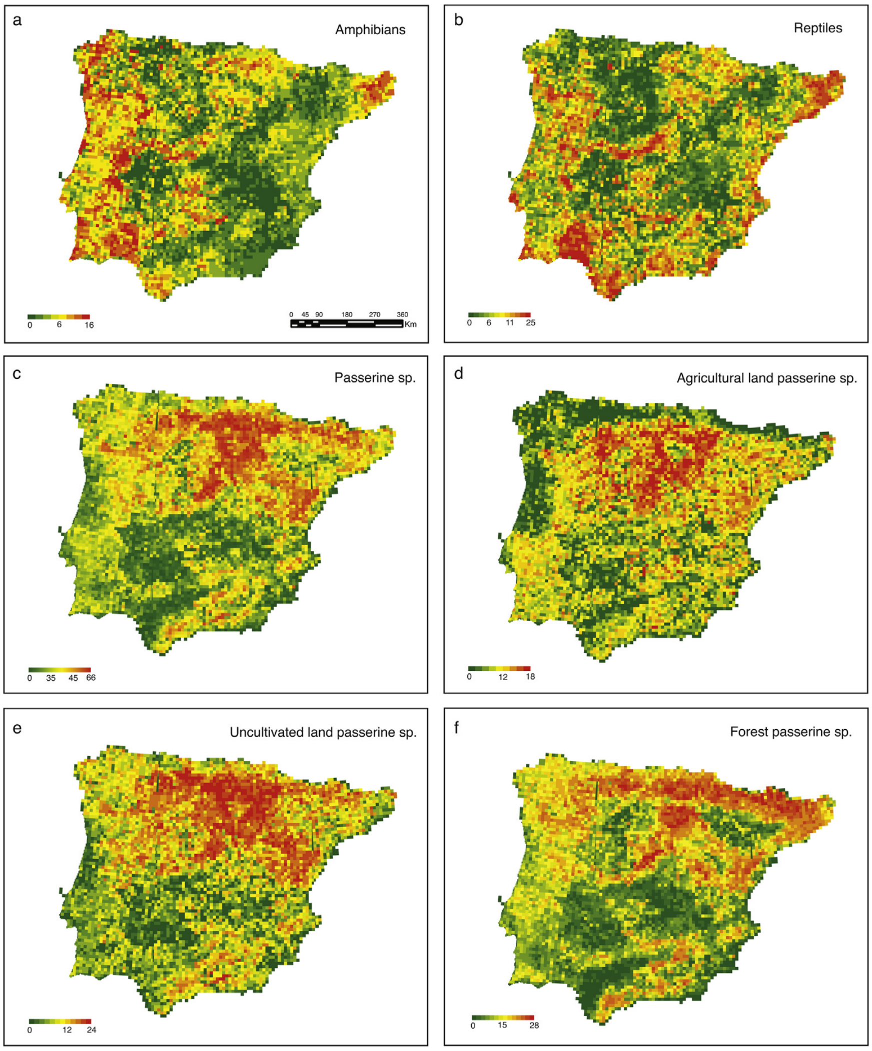

Fig. 1. Maps of species richness using a grain size of 10 km × 10 km: (a) amphibians ($n = 31$), (b) reptiles ($n = 64$), (c) all passerines ($n = 87$), (d) agricultural land passerines ($n = 19$), (e) uncultivated land passerines ($n = 32$), and (f) forest passerines ($n = 36$). Color scales are based on quantiles. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

We defined three groups of predictor variables: climate predictors, topographic predictors and habitat predictors. To test the effect of climate we considered: (1) mean temperature in July, (2) annual temperature range and (3) annual precipitation, in each cell. Topographic predictors were represented by: (4) mean elevation, (5) mean radiation, and (6) range of radiation. Finally, habitat predictors were represented by the percentage of main land cover categories: (7) agricultural land, (8) uncultivated land, (9) forest and (10) exotic forest (see Table A.2 for more details).

2.3. Data analysis

2.3.1. Effect of habitat heterogeneity on species richness

In order to explore the relationship between the three taxa (i.e., amphibians, reptiles and passerine birds) and habitat heterogeneity, a Spearman's rank correlation analysis between species richness and the number of habitats per cell was carried out. For an estimation of the shape of this relationship, we used LOWESS regression models as implemented in R 2.15.3 (R Development Core Team, 2013). We tested two spatial grids, the UTM grid of 10 km × 10 km and the UTM grid of 50 km × 50 km, and used the number of natural and human-modified land cover classes per UTM cell as an indicator of habitat heterogeneity. We only used the Spanish IFN2 land cover map in this analysis, because the number of land cover classes in the map for the Iberian Peninsula was too low after the harmonization of the two original land cover maps (IFN2 and COS90). The Spanish land cover map comprises 56 land cover classes (an average of 5 habitats per UTM cell, Table A.1) and was better suited for this analysis. The final sample set for this analysis comprised 3970 UTM cells at a 10 km × 10 km resolution and 136 UTM cells at a 50 km × 50 km resolution.

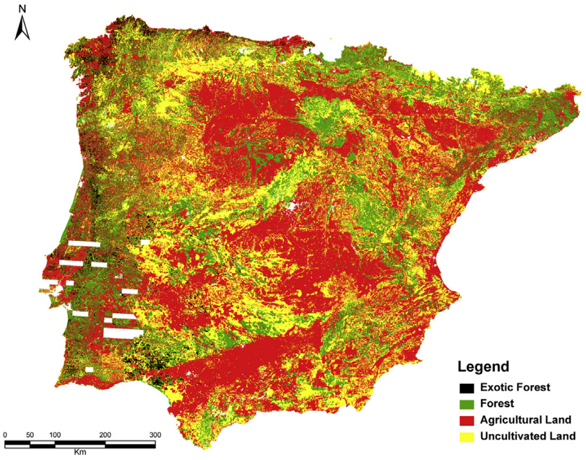

Fig. 2. Land cover map of the Iberian Peninsula. Blank cells indicate missing data.

2.3.2. The added value of land use variables: multimodel inference

First, the individual effect of climatic, topographic and habitat variables on species richness at the Iberian Peninsula scale was explored by determining the Spearman's rank correlation between single predictor variables and species richness. Then, we tested the additive effect of the three sets of explanatory variables using a multimodel selection and inference approach (Burnham and Anderson, 2002). We built a limited *a priori* model set to examine the effect of all variables considered. We tested models with a single set of predictors (i.e., only climatic variables (M_C), only topographic variables (M_T), and only habitat variables (M_H)). Afterwards, we tested combinations of different group variables: climatic plus topographic (M_{CT}), climatic plus habitat (M_{CH}) and topographic plus habitat (M_{TH}), and lastly, we tested all environmental variables together (M_{CTH}) (see Table A.2 for details about the different competing models). Ordinary least square (OLS) regressions (i.e., non-spatial models) were first used to fit the models. The presence of SA in the residuals of the regression models can violate the assumption of independently distributed errors and lead to shifts in parameter estimation and increases of Type I errors (Dormann et al., 2007). Therefore, we inspected spatial autocorrelation in the residuals of the OLS using Moran's *I* coefficient. The correlograms for 20 distance classes indicated significant spatial autocorrelation for all OLS models, regardless of the taxonomic group (Fig. B.1). In order to attenuate this problem, we also applied simultaneous autoregressive models assuming spatial autocorrelation in the error term (AR), to the same *a priori* model set. Model selection was based on model fit using Akaike information criterion (AIC; Akaike, 1973). We report ΔAIC, which is the difference between the evaluated model AIC and the lowest AIC among the tested models. The results from both non-spatial OLS models and AR models were interpreted and compared in our study. We also tested OLS with models including second-order polynomials for each variable; the relative model ranking was similar to the AR models (results are presented in Table A.3).

Variation partitioning was used to assess the individual and shared contributions of each set of explanatory variables. We decomposed the fitted AR models, into the non-spatial and the spatial trends, and only the non-spatial trends were used for variation partitioning, since we primarily focused on the pure explanatory power of each set, particularly habitat, rather than on their mixed effects with space (Xu et al., 2014). Because R^2 values are not directly provided for AR models, model fit was assessed using Nagelkerke pseudo-R^2 (hereafter simply referred to as pseudo-R^2). All analyses were implemented in R 2.15.3 (R Development Core Team, 2013), spatial models were fit using the *spdep* package (Bivand et al., 2013).

2.3.3. The added value of land use variables: species-area models

We explored the contribution of land use data to estimate species richness at the Iberian Peninsula scale using species–area relationships. Species-area models have been widely used to study the response of species to habitat loss (Reid, 1992; van Vuuren et al., 2006). We compared the fit of the classic species–area relationship (Arrhenius, 1921), which is a single-habitat SAR (i.e., it uses a single variable to describe the size of the area), with the fit of a multi-habitat model, the countryside SAR (Pereira and Daily, 2006). The SAR is usually expressed by the power law $S = cA^z$, where S is the number of species in a sampling area of size A, c and z are constants that depend on the taxonomic group and sampling scheme respectively (Rosenzweig, 1995; Crawley and Harral, 2001). The countryside SAR builds on the classic SAR and its application requires two steps. First the countryside SAR estimates the species richness of groups composed by species with similar habitat preferences, Eq. (1), where S_i is the number of species in group i, h_{ij} is the affinity of species group i to habitat j and A_j is the area cover by habitat j:

$$S_i = c_i\left(\sum_j h_{ij}A_j\right)^z \quad (1)$$

Then, the total number of species in the landscape, S_i, is given by the sum of species in each group (Eq. (2)), where m is the number of species groups:

$$S = \sum\nolimits_{i=1}^{m} S_i \quad (2)$$

Species-area models were applied to passerine data, divided into species groups according to their habitat preferences. We opted to use only data from passerines (i.e., excluding amphibians and reptiles) since they were the group most prone to be categorized in such a way. Data on habitat preferences were extracted from the literature (Pleguezuelos et al., 2002; Martí and del Moral, 2003; Equipa Atlas, 2008; Catry et al., 2010). We classified 19 species as agricultural land passerine species, 32 species as uncultivated land passerine species and 36 species as forest passerine species (Fig. 1; see Table A.4 in Supplementary Information for the complete species list). The data used to build the SAR models were obtained through the aggregation of species richness and land cover data in 10 km × 10 km UTM cells, into three new grains: 50 km × 50 km (261 cells), 100 km × 100 km (90 cells) and 200 km × 200 km (29 cells). The alignment among the different grain grids was adjusted to preserve the greatest number of cells possible. We fitted the SAR models using the *nls* function from the *stats* package in R. We estimated the parameters c and z for both models, and the affinities h_{ij} for the countryside SARs; see Proença and Pereira (2013) for more details on model fitting. We ranked and compared the fitted models using the AIC and the Root Mean Square Error (RMSE; Levinson, 1947), with lower values of RMSE and AIC indicating better fit to data (Sakamoto et al., 1987).

3. Results

Species richness patterns in the Iberian Peninsula vary with taxa (Fig. 1). The areas with higher number of amphibian species are concentrated in the western region of Iberian, in the Central mountain range and across Catalonia. The areas of high species richness for reptiles are mainly located in southern Spain, in the central region of Iberia (i.e., Central mountain range and Extremadura) and across Catalonia. Passerine species richness increases from south to north, and appears to be particularly associated with mountain regions.

3.1. *Correlation between species richness and environmental variables*

The response of species richness to habitat heterogeneity varied with cell grain size. At a spatial resolution of 10 km × 10 km, species richness of all taxa increased with increasing habitat heterogeneity (Fig. 3). Passerine species showed the strongest response to habitat heterogeneity (*rho* = 0.47), while reptiles species showed the weakest response (*rho* = 0.19). For amphibians and reptiles this increase was close to linear, but at a slower rate in the case of reptiles. On the other hand, the relationship between passerines and habitat heterogeneity seems to slow down or even stabilize at intermediate to higher levels of heterogeneity. At the spatial resolution of 50 km × 50 km, the richness of amphibians and reptiles did not show a significant relation with habitat heterogeneity (respectively, *rho* = 0.06 and *rho* = 0.04), while passerine species showed a strong positive relationship (*rho* = 0.58).

The relationship between single predictor variables and species richness varied among species groups (Table 1). Amphibian and reptiles showed similar responses to predictors, species richness increased with precipitation (*rho* = 0.40, *rho* = 0.20) but decreased with temperature range (*rho* = −0.33, *rho* = −0.21) and elevation (*rho* = −0.17) (Table 1). The richness of passerine birds increased with elevation (*rho* = 0.48) but decreased with mean radiation index (*rho* = −0.43) and both mean temperature and temperature range (*rho* = −0.19, *rho* = −0.57). In addition, there was an overall positive response of all taxa to natural habitat cover (i.e., forest and uncultivated land; 0.12 < *rho* < 0.36) and negative response to agricultural land cover (−0.29 < *rho* < −0.26). The response to exotic forest cover varied: passerines responded negatively (*rho* = −0.27), amphibians positively (*rho* = 0.32) and reptiles showed a weak response (*rho* = 0.12).

Table 1
Values of correlation (rho) between species richness and climatic, topographic and habitat predictors, at the grain size of 10 km × 10 km. ($p < 0.001$ for all the significant relationships; n.s. − non significant).

	Amphibians	Reptiles	Passerine birds
Mean temperature in July	−0.13	0.08	−0.57
Annual temperature range	−0.33	−0.21	−0.19
Annual precipitation	0.40	0.20	0.23
Mean elevation	−0.17	−0.17	0.48
Mean radiation index	$-0.02^{n.s}$	0.21	−0.43
Radiation index range	0.13	0.26	0.36
Agricultural land	−0.28	−0.26	−0.29
Uncultivated land	$0.01^{n.s}$	0.12	0.21
Forest	0.34	0.22	0.36
Exotic forest	0.32	0.12	−0.27

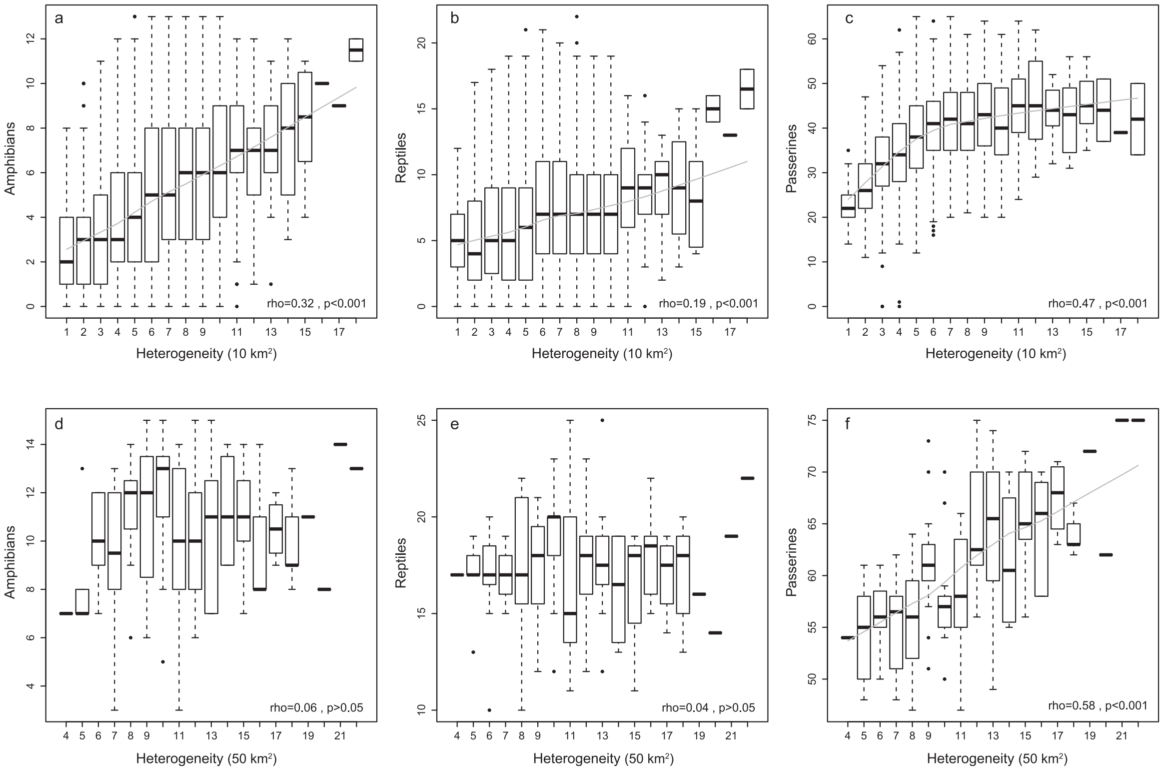

Fig. 3. Relationship between the richness of the different groups and landscape heterogeneity (estimated as number of land cover types per cell) for the 3970 cells of 10 km × 10 km: (a) amphibians, (b) reptiles, (c) passerines; and for the 136 cells of 50 km × 50 km: (d) amphibians, (e) reptiles, and (f) passerines; n.s = not significant. LOWESS regression lines are shown for the significant relationships.

3.2. *The added value of land use variables: multimodel inference*

The performance and estimate coefficients of all ordinary least square (OLS) models, and simultaneous autoregressive (AR) models are shown in Table 2. Compared with OLS models, AR models significantly reduce spatial autocorrelation (SA) (Fig. B.1). If we only considered models including one set of variables, that is, climate (M_C), topographic (M_T) or habitat (M_H) variables, the richness of amphibians and passerines was better explained by climatic variables while the richness of reptiles by topographic variables, thus indicating which set of variables have the main explanatory effect (Table 2, Table A.5). When the models including two sets (M_{TC}, M_{CH}, M_{TH}) and all sets of variables (M_{CTH}) were also considered, the M_{CTH} model was always the best model (i.e., smaller AIC values; Table 2, Table A.5). The second best models vary with taxa: for amphibians it was M_{CH}, which includes habitat variables in addition to climate variables; for passerines and reptiles it was M_{TH}, which includes both climatic and topographic variables. Focusing only on the explanatory power for the non-spatial trends of species richness (indicated by R^2 for OLS models and by pseudo-R^2 for the non-spatial components of the AR models; Table A.5) the influence of habitat seems to increase. In this setting, the second best model for all taxonomic groups was the one including habitat variables in addition to the main predictors. The variation partitioning analysis shows the relative importance of each set of variables in explaining species richness patterns (Fig. 4, Table A.6). When we considered the individual variance explained by each set of factors, the share of variance explained by habitat variables (5–22%) was relevant if compared with that of climatic (4–29%) and topographic variables (0.1–30%). For all taxonomic groups, the contribution of habitat variables was always second best to the contribution of the dominant predictor. The large mixed fractions of explained variation between sets of variables suggests an overlap between climatic, topographic and habitat variables. This was particularly evident in the case of passerines, were the combination between topographic and climatic variables explains more variance than all individual fractions.

3.3. *The added value of land use variables: species-area models*

Countryside SAR models showed a better fit (i.e., lower RMSE and AIC values) than classic SAR models, for all species groups and for the total number of species across the landscape (Table 3). Countryside SAR models yielded higher *c*-values than classic SAR models, but *z*-values were similar for the two model approaches. Species groups associated with open habitats (i.e., agricultural land and uncultivated land species) show moderate affinity to other habitats ($0.20 < h < 0.60$) than their preferred habitat. Forest species appear to be less tolerant to alternative habitats, showing low affinity to uncultivated land ($h < 0.01$) and agricultural land ($h < 0.00001$). An analysis on the correlations between the richness of each species group and the proportion of land cover types in each cell further supported these findings. Forest and uncultivated land passerine species showed a positive relationship with forest (*rho* = 0.58, *rho* = 0.13) and uncultivated land (*rho* = 0.24, *rho* = 0.21) and a negative relationship with agricultural land (*rho* = −0.51, *rho* = −0.13) and exotic forest (*rho* = −0.11, *rho* = −0.33). Agricultural passerines showed a positive relationship with agricultural land (*rho* = 0.12), a negative relationship with exotic forest (*rho* = −0.26), and no significant relationship with the remaining land cover types.

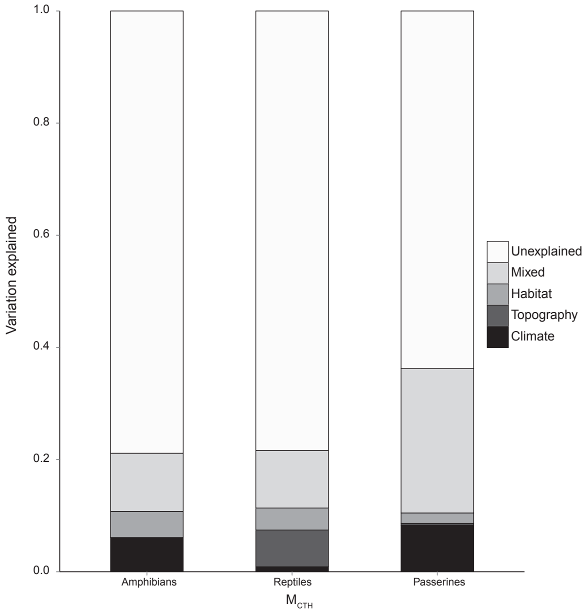

Fig. 4. Variation partitioning based on the non-spatial trend of the simultaneous autoregressive model for the model with the 3 sets of variables (M_{CTH}): Climate, variation purely explained by climate; Topographic, variation purely explained by topography; Habitat, variation purely explained by habitat; Mixed, variation shared between climate, topography and habitat; Unexplained, unexplained variation.

Table 2

Performance of the ordinary least square (OLS) and simultaneous autoregressive (AR) models on explaining the richness patterns of each taxonomic group at the grain size of 10 km × 10 km. Model designation refers to the different sets of predictors (climate (M_C), topographic (M_T) or habitat (M_H)), considered separately and jointly (in all cases $P < 0.001$). Multiple R^2 for OLS models and Nagelkerke pseudo-R^2 values for AR models are indicated; ΔAIC values and the lowest AIC (in parentheses) for each taxonomic group are also shown.

Model	Amphibians				Reptiles				Passerines			
	OLS		AR		OLS		AR		OLS		AR	
	R^2	ΔAIC	R^2	ΔAIC	R^2	ΔAIC	R^2	ΔAIC	R^2	ΔAIC	R^2	ΔAIC
M_C	0.17	477	0.54	44	0.10	953	0.51	231	0.33	434	0.60	150
M_T	0.06	1187	0.53	144	0.17	430	0.52	110	0.29	770	0.60	180
M_H	0.15	587	0.53	141	0.08	1101	0.51	269	0.13	1967	0.60	264
M_{CT}	0.18	387	0.54	27	0.21	214	0.53	46	0.35	257	0.61	59
M_{CH}	0.22	81	0.54	10	0.18	380	0.52	148	0.37	107	0.61	70
M_{TH}	0.18	375	0.53	103	0.22	108	0.53	63	0.32	498	0.61	121
M_{CTH}	0.23	$0^{(29,454)}$	0.54	$0^{(26,434)}$	0.23	$0^{(33,417)}$	0.53	$0^{(30,504)}$	0.38	$0^{(40,474)}$	0.61	$0^{(37,675)}$

Table 3

Species–area relationships of passerine birds (for species groups and total species) using the classic model (SAR) and the countryside model (CSAR). A total of 6265 cells, including all cell grain sizes, were used in the analysis. Parameters h_{AL}, h_{UL}, and h_F represent the affinity of the species groups for agricultural land, uncultivated land and forest respectively; c and z are model parameters. The countryside species–area relationship for total species is expressed by the sum of species–area relationships of species groups. RMSE and AIC are indicated to compare the fitness of the models.

	c	z	h_{AL}	h_{UL}	h_F	RMSE	AIC
Agricultural Land species							
SAR	1.74	0.102	–	–	–	2.55	11,754
CSAR	1.84	0.101	1	0.60	0.31	2.54	11,696
Uncultivated Land species							
SAR	0.56	0.165	–	–	–	3.70	16,409
CSAR	0.67	0.162	0.20	1	0.36	3.64	16,210
Forest species							
SAR	1.01	0.144	–	–	–	5.06	20,326
CSAR	1.86	0.126	0.59×10^{-6}	0.74×10^{-2}	1	4.00	17,378
Total species							
SAR	2.90	0.139	–	–	–	9.41	28,096
CSAR	$S_{\text{total}} = S_{\text{agriculture land}} + S_{\text{uncultivated land}} + S_{\text{forest}}$					8.56	26,922

4. Discussion

4.1. Species richness response to land use variables

Understanding the effects of land use change, namely habitat loss and changes in habitat composition, on the distribution of species richness is a fundamental step in conservation planning (Foley et al., 2005). Our results show that the relationship between habitat heterogeneity and species richness varies with taxa and grain. At a 10 km × 10 km resolution, all taxa responded to habitat heterogeneity. Previous studies, conducted at similar or finer scales, have reported similar results (reviewed in Tews et al., 2004). On the other hand at the 50 km × 50 km grain size, the richness of amphibians and reptiles shows no significant trend with habitat heterogeneity. Although is well accepted that habitat heterogeneity promotes species richness by increasing opportunities for niche partitioning (Kadmon and Allouche, 2007), there are large differences between the spatial resolutions at which individuals experience the environment and on their response to changes in habitat size and heterogeneity in the landscape. That is, species use structural characteristics of the habitat that occur on a specific scale, reflecting important habitat requirements such as shelter, foraging or reproduction niches (Mazerolle and Villard, 1999; Atauri and de Lucio, 2001; Gil-Tena et al., 2007; Desrochers et al., 2011). The presence or quality of this specific structure may then determine species richness of a particular group. In the case of amphibians and reptiles, a 10 km × 10 km grain size, probably covers most of the relevant habitats for these species while also encompassing habitats that maintain the minimum size to sustain viable populations. Our results suggest that an increase in spatial resolution to 50 km × 50 km is not accompanied by an increase in habitat heterogeneity as perceived by these taxa. In the case of passerines, their higher mobility is also reflected on their habitat requirements, namely on larger habitat sizes. The shape of the relationship between passerines richness and habitat heterogeneity seems to follow the pattern predicted by the area-heterogeneity trade-off hypothesis. Kadmon and Allouche (2007) stated that any increase of environmental heterogeneity within a fixed space must lead to a reduction in the average amount of effective area available for individual species and, thus, increase the likelihood of stochastic extinctions. One can argue that at a 10 km × 10 km spatial resolution the inflation point for passerines (i.e., the level of heterogeneity that maximizes species richness) has been reached, there is an equilibrium between the likelihood of successful colonization, by providing suitable conditions to a large number of species, and the likelihood of stochastic extinctions, by reducing the amount of effective area available for individual species. However, at a 50 km × 50 km spatial resolution the shape of the relationship between passerines and habitat heterogeneity is constantly positive, suggesting that, at this grain size, area is yet to become a limiting factor and species richness monotonically increases with habitat heterogeneity. Notwithstanding, our results for amphibians and reptiles may have been constrained by the available data. In fact, the habitat classification used, that is, the Spanish IFN2 and forest types, may be more suitable to model passerine response to habitat heterogeneity than to model amphibians or reptiles response, which may be more sensitive to other habitat features than dominant tree coverage.

The negative relationship of all taxa to the area of agricultural land corroborates the findings of studies at smaller scales showing the importance (positive or negative) of human-modified habitats for vertebrate species, namely amphibians (Beja and Alcazar, 2003; Stuart et al., 2004; Piha et al., 2007; García-Muñoz et al., 2010), reptiles (Ribeiro et al., 2009) and birds (Green et al., 2005; Wretenberg et al., 2006).

4.2. The added value of land use variables

While our results agree with studies showing that climate is the main determinant of species richness at large spatial extents (Hawkins et al., 2003; Moreno-Rueda and Pizarro, 2009; Triviño et al., 2011; Luo et al., 2012), there was also evidence on the importance of land use variables. As mentioned before, the relative importance of climate and land use variables when explaining species richness patterns is commonly considered as hierarchically scale-dependent (Rahbek and Graves, 2001; Thuiller et al., 2004; Rahbek, 2005). Our results from the OLS and AR models support the current knowledge that at larger scales, when climate and land use variables are individually considered, climate variables tend to yield models with higher explanatory and predictive values (González-Taboada et al., 2007). However, our findings also show that land use variables can be combined with main predictors, such as climate (Luoto et al., 2007; Moreno-Rueda and Pizarro, 2009; Xu et al., 2014) and topographic (Moreno-Rueda and Pizarro, 2007; Reino et al., 2013) variables, to improve the descriptive power of models.

The increase of the overall model fit, when taking land use variables into consideration, could be either a consequence of the large spatial scale or of the better resolution of land use data. For example, Thuiller et al. (2004) showed that land cover data did not improve model accuracy in Europe. However, they pointed out that the insufficient resolution of their data could mask the effect of habitat heterogeneity. They worked at a 50 km × 50 km spatial resolution with land cover data originally developed at a spatial resolution of 1 km. More recently, Triviño et al. (2011) working with Iberian birds richness in a 10 km × 10 km resolution reported that only in few cases did the vegetation and landscape configuration variables contributed to improve the fit of the models. Triviño et al. (2011) cautioned that the land cover data used (i.e., Corine Land Cover (CLC)) were a rather coarse proxy of the habitats important for birds. In our study, although we use the same spatial resolution, the use of national land cover datasets, which have finer spatial resolution (e.g. COS 90 map has a minimum mapping unit of 1 ha at a 1:25 000 scale) than the land cover datasets used in similar studies (e.g. CLC 2006 map has a minimum mapping unit of 25 ha a a 1:100,000 scale), presumably allowed us to detect a stronger habitat signal in the models. Furthermore, these national land cover datasets were used in intermediate scale studies (i.e., covering areas between 8000 km^2 and 16,000 km^2) where habitat was consistently found to be the most important determinant of species richness (Atauri and de Lucio, 2001; Nogués-Bravo and Martínez-Rica, 2004; Moreno-Rueda and Pizarro, 2007).

Results from SAR models, showed that the species richness of passerine species groups and the total number of passerine species were better described by the multi-habitat model. The countryside species–area relationships accounts for land use information and for species affinity for the different land uses in the landscape. The better fit of the countryside model supports our hypothesis on the role of habitat as a key determinant of species richness patterns, and agrees with the results from the other analyses performed in this study.

The parameters of the countryside models reflect the species abilities to use alternative land uses. Relative to the classic SAR outputs, *c*-values increased and *z*-values kept stable or slightly decreased, suggesting a stronger dynamics of species between habitats, with inter-patch movements that keep high levels of local species richness and stabilize the rate of species accumulation with increasing area. The parameters of the countryside model also reveal a strong response of passerine species groups to habitat type. Although all species groups showed a higher affinity to their preferred habitat, they also present a relatively good affinity to non-preferred habitats, with forest species being the less tolerant to alternative habitats, and agricultural species the more tolerant to non-agricultural habitats. Many studies have highlighted the importance of non-agricultural habitats in maintaining agricultural biodiversity, by providing nesting and foraging habitats (Hinsley and Bellamy, 2000; Herzon and O'Hara, 2007; Vickery and Arlettaz, 2012).

5. Conclusion

Major gaps and uncertainties remain when trying to explain species richness patterns (Pereira et al., 2012). Our findings suggest that in addition to the predominant effect of climate, habitat variables also affected species richness patterns of terrestrial vertebrate in the Iberia Peninsula.

With land use change being a dominant driver of global biodiversity change (Leadley et al., 2010; Pereira et al., 2010), its incorporation in modeling approaches is of major importance for future scenario analysis and conservation planning. Our study shows that land use related variables could add relevant information to current modeling frameworks, and therefore, should also be considered, when assessing species richness patterns at large scales. Finally, it is important to recognize the role of the resolution at which dependent and response variables are recorded; having high resolution data across scales will undoubtedly help the efforts to accurately quantify how environmental conditions influence species richness patterns and their underlying processes.

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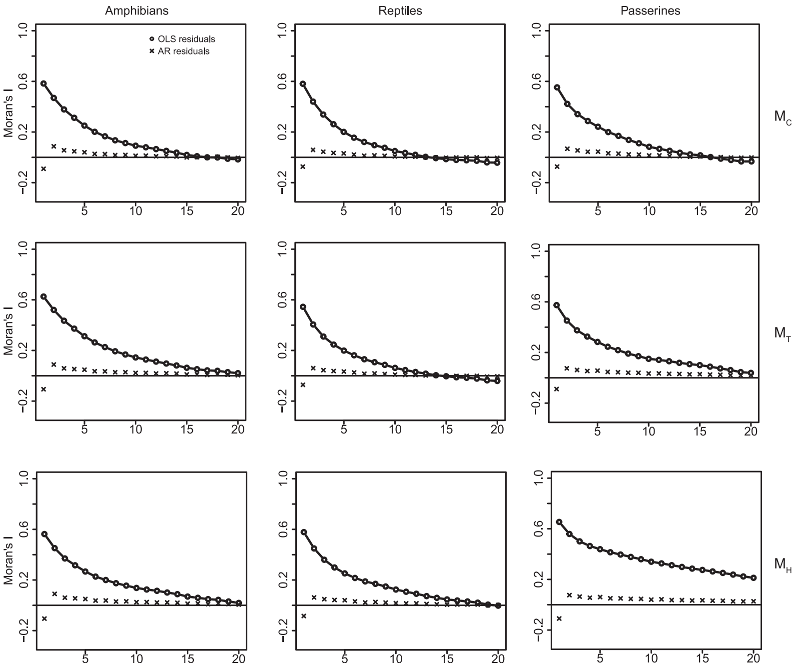
Appendix A. Supplementary data

Supplementary data related to this article can be found at http://dx.doi.org/10.1016/j.actao.2014.10.005.

Appendix B



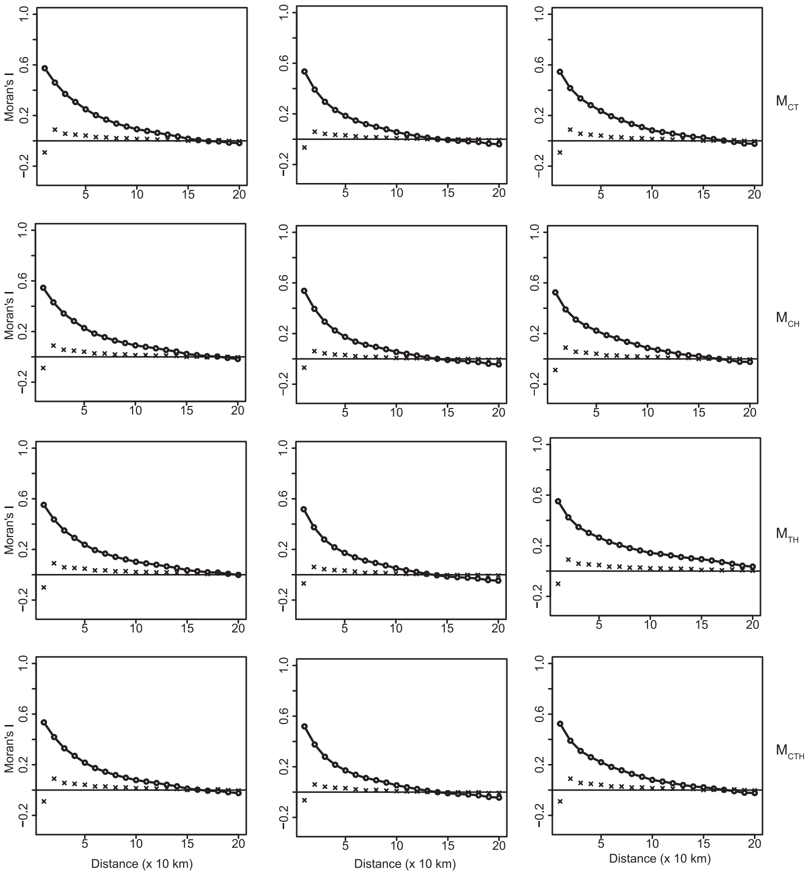


Fig. B.1. Correlograms for residuals from ordinary least square (OLS) and simultaneous autoregressive models (AR) for all models and groups tested.

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Chapter 3

Improving extinction projections across scales and habitats using the countryside species-area relationship

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Improving extinction projections across scales and habitats using the countryside species-area relationship

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The species-area relationship (SAR) has been often used to project species extinctions as a consequence of habitat loss. However, recent studies have suggested that the SAR may overestimate species extinctions, at least in the short-term. We argue that the main reason for this overestimation is that the classic SAR ignores the persistence of species in human-modified habitats. We use data collected worldwide to analyse what is the fraction of bird and plant species that remain in different human-modified habitats at the local scale after full habitat conversion. We observe that both taxa have consistent responses to the different land-use types, with strongest reductions in species richness in cropland across the globe, and in pasture in the tropics. We show that the results from these studies cannot be linearly scaled from plots to large regions, as this again overestimates the impacts of land-use change on biodiversity. The countryside SAR provides a unifying framework to incorporate both the effect of species persistence in the landscape matrix and the non-linear response of the proportion of species extinctions to sampling area, generating more realistic projections of biodiversity loss.

Globally, habitat loss and habitat degradation are identified as the main current threats to vertebrates, affecting more than 80% of globally threatened mammals, birds, amphibians and plants[1]. Assessing the response of species to different scenarios of land-use has become essential to predict patterns of species extinction and guide conservation actions[2]. Species-area relationship (SAR) models have been often at the heart of such assessments, projecting species extinctions as a consequence of loss of area of native habitat[3–5].

The SAR is one of the oldest known patterns in ecology and has been studied in a wide variety of systems and scales[6]. Although a range of functions have been proposed to model the SAR, a power function relating the number of species S with the area of habitat A, $S(A) \sim A^z$, is most commonly used to assess species extinctions after habitat loss. Therefore, if an area a of the original native habitat is converted to human-modified habitat, the fraction of species that is predicted to go extinct (ε) is given by[7]

$$\varepsilon(a) = \frac{S(A) - S(A - a)}{S(A)} = 1 - \left(\frac{A - a}{A}\right)^z, \tag{1}$$

where z is a constant indicating the rate at which species richness increases with area.

Despite its widespread use, this technique has a number of limitations, leading to a mismatch between predicted extinctions and recorded extinctions[8,9]. Some studies have pointed that extinction estimates generated using the SAR are often greater than those from empirical data (e.g.[10,11]), while others argue that the SAR may actually underestimate species extinctions in the long run, particularly in highly fragmented landscapes (e.g.[12,13]). This debate is not yet settled as there are still unresolved issues. One issue is the extinction debt, i.e. the difference between the immediate extinctions of the species restricted to the area of lost habitat and the future extinctions of species which cannot persist in the long-term on the area of remaining habitat[7,14]. Some studies have argued that

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these two distinct extinction processes are described by different types of SAR, with the latter having a steeper slope[6,7,15]. Others have argued that the SAR can only be used to estimate immediate extinctions[11,16].

Another issue, that we believe to be even more prevalent, is that many species are able to persist in human-modified habitats. In contrast, the classic SAR assumes that human-modified areas (e.g. agricultural lands) are completely hostile to biodiversity[7,17]. Some recent global biodiversity models address this problem by estimating extinctions based on empirical studies of local species richness response to habitat conversion[18,19]. However, they do not account for how the impacts of land-use change on biodiversity may vary non-linearly with the spatial grain of analysis[20].

This third issue has not been appreciated until now and is a distinct conceptual problem from the well-known non-linear relationship between species extinctions and proportion of remaining habitat. For instance, according to the classic SAR (equation (1)), when 90% of the habitat is lost in a landscape, and assuming a z of 0.20, only 37% of the species are lost (global extinctions). However, one may ask if the same proportion of species go extinct in a small plot in the landscape (local extinctions).

The issue of extinction debt has been discussed in many papers (e.g.[21–23]) and we will not revisit it here. Instead, here we discuss how the countryside species-area-relationship provides a framework to project short-term species extinctions that take into account species persistence in the matrix and the non-linearity of species extinctions with sampling scale. Short-term projections may underestimate the long-term consequences of habitat loss but are perhaps more consistent with policy relevant time scales.

The countryside species-area relationship

The classic SAR only captures the species richness response to changes in native habitat area, overlooking the diversity of species responses to changes in habitat composition. In order to address this problem Pereira and Daily[24] proposed the countryside SAR. Although there have been other SAR models trying to account for the response of biodiversity to different habitat types[10,25,26], the countryside SAR model is the only one that accounts for the differential use of habitats by different species groups. In the countryside SAR, the richness of each species group i, S_i, is given by a function of the area of each habitat j in the landscape,

$$S_i(A_1, A_2, \ldots, A_n) = c_i\left(\sum_{j=1}^{n} h_{ij}A_j\right)^z, \tag{2}$$

where n is the number of habitat types, h_{ij} is the affinity of the species group i to habitat j, A_j the area of habitat j, and c_i measures the relative local abundance of each species group i. Then, the total number of species in the landscape, S, is given by the sum of all species groups. For simplicity, we use a power function to describe the countryside SAR (equation (2)) as this is the model typically used to predict species extinctions by area reduction, but whether other functions better describe the shape of the countryside SAR at different sampling scales is still an open question[27–29].

Consider a single functional group (i.e. dropping the subscript i in equation (2)) and only two habitats, native ($j = 1$) and modified habitat ($j = 2$). Then, if an area a of a landscape of size A is converted, the fraction of species extinctions is

$$\varepsilon(a) = \frac{S(A, 0) - S(A - a, a)}{S(A, 0)} = 1 - \left(\frac{h_1\,(A - a) + h_2 a}{h_1 A}\right)^z. \tag{3}$$

The countryside SAR predicts that some species always remain in the landscape (as long as $h_2 > 0$). The proportion of species remaining will depend on their affinity to the human-modified habitats, h_2. The countryside SAR describes the relationship between species richness and habitat area better than the classic SAR, both at local[28,30] and regional scales[31], and it also projects species extinctions more accurately[32].

Estimating the affinity of biodiversity to human-modified landscapes

A key parameter of the countryside SAR is the affinity of species to each habitat, h_j. Affinity values can be estimated from local data studies (i.e. studies carried out at plot size scale). Let σ_j represent the sensitivity[10] of species to the full conversion of native habitat into the modified habitat j, i.e. the proportion of species disappearing at the plot-scale in modified habitats:

$$\sigma_j = 1 - \frac{S(j)}{S(1)}, \tag{4}$$

where $S(1)$ and $S(j)$ represent species richness at the plot scale in the native and modified habitat of type j, respectively. Note that σ_j equals ε (equation (3)) at the plot scale when the native habitat is fully converted to habitat j (i.e. $a = A$). It can be shown that $h_j = (1 - \sigma_j)^{1/z}$ [32], since affinities and sensitivities are related (see Supplementary Note). A fully hostile modified habitat where all species go extinct corresponds to a sensitivity of one, while a fully hospitable modified habitat corresponds to a sensitivity of zero. It is also possible to have a negative sensitivity when the modified habitat has higher species richness than the native habitat (e.g. exotic species colonize the modified habitat).

We examined the distribution of sensitivities of birds and plants to habitat conversion into different land-use types in two distinct climate regions (Fig. 1) and estimated the corresponding habitat affinities for the countryside SAR. For such analysis we used two previously published databases of local studies from across the globe where $S(1)$ and $S(j)$ were reported[33,34] (see Supplementary Tables S1 and S2 and Methods). None of the taxon

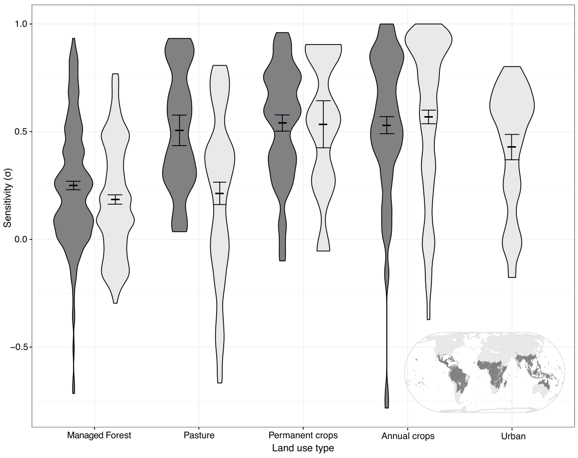

Figure 1. Local scale sensitivity (σ) of species in tropical (dark-grey; N = 355) and temperate (light-grey; N = 375) regions to the different human-modified habitats. The width and length of the polygons indicates, respectively, the density and range of the data. Error bars indicate standard errors. Inset map was created based on WWF terrestrial ecoregions[47] in order to highlight the two distinct climate regions using ArcGIS 10.2.1 software[48].

shows complete sensitivity to any of the transformed habitats (i.e. $\sigma = 1$). On average species respond better to the presence of managed forest and pastures than to the presence of crops, with some studies even reporting beneficial impacts (i.e. $\sigma < 0$). A three-way analysis of variance and an effect size analysis (see Supplementary Fig. S1) showed that while the effect of land-use was significant ($\eta^2 = 0.20$, $F_{4,712} = 46.58$, $p < 0.001$), the effect of taxon was non-significant. The interaction between these variables was also significant although small in effect (taxon × land-use type: $\eta^2 = 0.02$, $F_{4,712} = 3.87$, $p < 0.01$). In addition, species show similar sensitivities across the globe, but for some land-use types, the sensitivity may vary between tropical and temperate regions, as in the case of pastures (Fig. 1).

Scaling biodiversity response to habitat conversion from the local level to the regional scale

The next problem is how to scale the response of biodiversity to land-use change from the local scale, which was the scale of the studies used to estimate these sensitivities, to the larger scales at which we often want to make projections. While one expects, based on the classic SAR (equation (1)), that species extinctions scale non-linearly with area of habitat loss, what happens to species extinctions as one changes the scale of analysis (i.e. sampling grain) has not been assessed until now.

Consider a landscape represented by a grid where each cell can be either native habitat or human-modified habitat (Fig. 2 inset, Methods). One can sample this landscape at a given window size, Ω and calculate the average proportion of species extinctions across all sample windows as (Supplementary Fig. S2),

$$\overline{\varepsilon(\Omega)} = \frac{\sum_k \varepsilon(a_k^{\Omega})}{N(\Omega)}, \tag{5}$$

where a_k^{Ω} is the area of human-modified habitat in the window k of size Ω, and $N(\Omega)$ is the total number of windows of size Ω in the landscape. In order to calculate the species extinctions in each sampling window of the landscape, $\varepsilon(a_k^{\Omega})$, we used the countryside SAR (equation (3)), the classic SAR (equation (1)), and a linear model (countryside SAR with $z = 1$). The linear model assumes that the fraction of extinctions is directly proportional to the amount of habitat-modified times the species sensitivity ($\varepsilon(a) = \frac{a \cdot \sigma}{A}$, see Methods).

Using the linear model, the fraction of extinctions is constant across scales but is scale dependent for the countryside and classic SAR: the mean proportion of species extinctions decreases with increasing sampling scale for the two SAR models (Fig. 2). This suggests that the linear model overestimates the proportion of species going extinct at large scales. That is, the sensitivity of a taxonomic group to habitat change cannot be linearly extrapolated for scales other than those at which the study was conducted.

For a small sampling grain, the mean proportion of species extinctions estimated with the classic SAR approaches the proportion of human-modified habitat in the landscape (90% in Fig. 2, 50% and 10% in Supplementary Fig. S3). This proportion of extinctions is much higher than what is known to happen from the field studies at the local scale (linear model). This happens because the classic SAR assumes that the human-modified habitat is completely inhospitable (e.g. when 90% of the habitat is converted, local species richness becomes zero in 90% of the sites).

In contrast, in the countryside SAR matches the results from the field studies at the local scale (the linear model) and projects lower extinction rates at larger scales due to the non-linear relationship between habitat

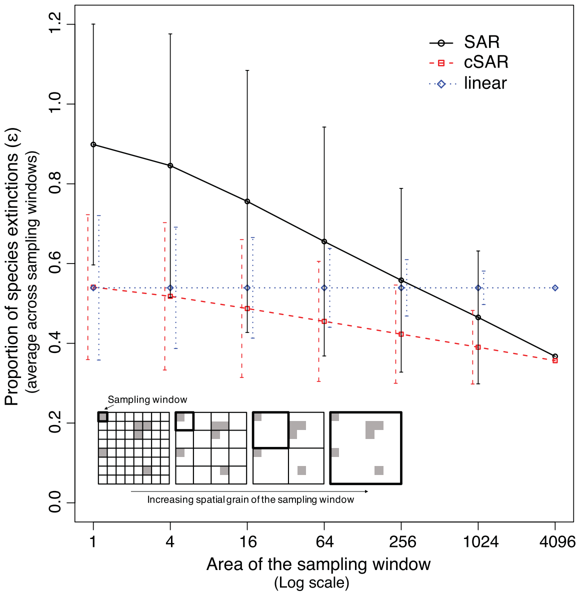

Figure 2. Proportion of species extinctions (ε) in the simulated landscape after 90% habitat conversion given by the linear, classic SAR and the countryside SAR. Points corresponds to the average number of species extinctions (across 1000 simulations) calculatsed in all sampling windows of a given sampling scale (a natural log transformation was applied to the area of the sampling window). Inset illustrates the nested sampling, with white squares corresponding to human-modified habitat and grey squares to the native habitat. For all models, $z = 0.2$, with, $h_1 = 1$ for the native habitat and $h_2 = 0.01$ for the modified habitat. Error bars indicate for each model, the standard deviation of the fraction of species remaining at a given sample grain.

area and species richness (Fig. 2). This pattern occurs independently of the amount of native habitat remaining in the landscape, of the rate at which species richness increase with area (z value), of the sensitivity of species to human modified habitats, and of the degree of fragmentation of the landscape (Supplementary Figs S3 and S4). In addition, the variance of the proportion of species extinctions across sampling sites decreases with increasing sampling scale (Fig. 2). This decrease in the variance of species extinctions with scale is fastest with the linear model and slowest with the classic SAR.

Discussion

SARs have been used to project biodiversity loss at regional to global scales but these projections ignore the persistence of species in human-modified landscapes. Here, we show that species response to habitat conversion vary significantly between land-use types, with some studies even reporting a positive response to human-modified habitats. We did not distinguish between specialist (i.e. occurring in only one habitat) and generalist species (i.e. occurring in more than on habitat), and while we can expect within taxon responses to vary among species functional groups (e.g. forest bird species, agriculture bird species), species are known to show dissimilar degrees of tolerance to habitat conversion, even among habitat specialists[35]. On average species respond better to the conversion of native habitat to managed forests and pastures than to cropland. Our finding corroborate those by Gibson *et al.*[36] and Newbold *et al.*[19] among others. Both studies found cropland areas to have some of the strongest global effects on biodiversity, although Newbold *et al.* identifies urban areas as the land-use with the highest effects on biodiversity loss. This is mostly due to a strong effect of land-use intensity in urban areas found by Newbold *et al.*, where urban areas are particularly hostile to biodiversity when intensively used, but have the lowest effects on biodiversity when minimally used. The sensitivity of species to urban areas seems to vary highly with the degree of land-use intensity[19].

Although we did not observe significant differences across taxa and region, we found that for some land-use types, the sensitivities may vary among plants and birds and between tropical and temperate regions. Birds species tend to be more sensitive to forest conversion into agriculture, whereas plants are more sensitive to burned forests and shaded plantations[36–38]. Furthermore, in some cases habitat conversion can lead to increase of richness of a taxon or a specific species group while decreasing the richness of another taxon or species group[39] (e.g. when forest is converted to cropland, farmland bird species may increase their richness while forest bird species decrease theirs). Several studies have highlighted that tropical regions, especially South America and Southeast Asia, are particularly vulnerable to all forms of human impact[36]. We found species to have similar sensitivities to habitat conversion in tropical areas and temperate areas, with species responding differently only to particular habitats, such as pastures (i.e. species more sensitive to pastures in tropical areas). This could be a result of the recent and widespread expansion of pasture areas in the tropics, whereas in temperate regions, such areas have existed for millenia[40].

Overall, the likelihood of species undergoing extinction following habitat loss will depend on their sensitivity to the modified habitat and the capacity of the modified habitats to support them[10,17,24,34]. Consequently, SAR-based extinction projections are only reliable for species with zero affinity for the human-modified habitats. Here, we have estimated habitat affinity values for a range of land-use types, which can then be used in conjunction with the countryside SAR to project biodiversity responses at scales larger than the plot scale for which field data was originally collected. The methodology used here to calculate habitat affinities can also be applied to other databases of biodiversity responses to land-use (e.g.[19]).

Empirical studies have suggested that as the spatial grain increases, the effect of land-use on biodiversity patterns tends to decrease[31], which may lead to the signal of land-use change being difficult to detect at large spatial scales. At very small scale the habitats are homogenous and one either counts species entirely within native or entirely within a human-modified habitat. In contrast at larger scales, any sampling unit is a mixture of both habitats and the non-linear effects of the SAR come into play.

To our knowledge, this non-linearity of the response of biodiversity to land-use change across sampling scales (or grain of analysis) has not been theoretically analysed before. Recently, Keil *et al.*[20] has shown that empirical extinction rates may vary with sampling area, using extinction data from plants and butterflies across the European continent and North America. Interestingly they showed that this variation may be non-monotonic with scale: number of extinctions at local and large scale may be similar, but lower or higher than the number of extinctions at intermediate scales, depending on whether the response curve is convex or concave. The number of extinctions is the product of the proportion of species going extinct with the number of species. We already knew that the number of species increases with sampling area, as predicted by the species-area relationship. If the proportion of species going extinct was constant with scale, this would result in a monotonic increase of the number of species going extinct with scale. Here we show that the proportion of species going extinct may decrease with increasing sampling scale. Therefore, our results are consistent with the findings of Keil *et al.*[20] of a non-monotonic relationship between number of extinctions and sampling scale.

This non-linearity of proportion of species extinction with sampling scale calls for some caution when interpreting maps of impacts of land-use change coming out of models such as GLOBIO and PREDICTS[18,19]. Studies using these models often plot the reduction in species richness using grid cells of 50 km × 50 km or larger based on plot level responses to land-use change. Our analysis suggests that the reductions at those scales may be significantly smaller than those at the plot scale, and therefore these maps should be interpreted as the plot-scale mean reduction in species richness. These maps are therefore not comparable with, for instance, analysis of changes of atlas of species distribution collected at those scales.

Furthermore, our results suggest that caution should be used when interpreting species richness trends from local studies. Recent global meta-analysis have found no reduction in species richness over time in time series of community assemblage data[41,42]. Hill *et al.*[43] used a simple narrative based model to show that there is a large variance in plot-based species richness and therefore it may be difficult to detect a decline in species richness, even when the decline is clear at the regional level. Similarly, we found that, when all the sites are aggregated in the analysis independently of whether habitat conversion has occurred or not, the variance in the proportion of species extinction estimates is very large. This detection problem is particularly exacerbated when the signal of species richness change is small due to only a small proportion of the habitats haven been converted.

The complexity of studying biodiversity change across scales and habitats should not be underestimated. It is empirically challenging and requires a solid theoretical background. Our study contributes to a deeper understanding of SAR models and their applicability when projecting species extinctions as a consequence of habitat loss. Finally, we demonstrate that the countryside species-area relationship[24] provides a unifying framework to account both for the effects of species persistence on the matrix and for the non-linearity of biodiversity response with scale. Improved global analyses of biodiversity loss are needed, specially to better inform future conservation goals (e.g. post- 2020 Aichi Targets) and ongoing policy-driven assessments (e.g. IPBES Global Assessment). The extinction projections from the countryside SAR may be less catastrophic but they are certainly more realist and will ultimately allow for better decision-making.

Methods

Studies used to estimate the affinity of biodiversity to human-modified landscapes.

Sensitivity values (σ) were taken from two previously published global databases[33,34] of studies of biodiversity responses to human-modified landscapes. From within these databases, we selected studies that provided data on bird and plants species richness on both native habitat and at least one human-modified habitat. In several of these studies, data for multiple habitat types, locations and/or species groups were reported, which led to a total of 730 pairwise comparisons. The databases do not distinguish between specialist species or generalist species, as in most cases the number of species in a given habitat was the only data reported. The data was subset into five land-use classes based on the description of the habitat given in the source paper: annual crops, managed forest, permanent crops, pastures and urban; and two major biomes: tropical and temperate. For all studies (see Supplementary Table S1) the databases report the sensitivity of a taxonomic group to habitat j, σ_j, as the difference between the plot scale species richness found in the modified habitat of type j and the species richness in the native habitat (see equation (4)). Habitat affinities can be directly derived from these sensitivities (see Supplementary Note for details).

Models for scaling the biodiversity response to habitat conversion.

To demonstrate and analyse the effect of sampling scale on extinction projections, we simulated 1000 spatially-explicit landscapes represented on a lattice of 64 × 64 grid cells (inset Fig. 2). We randomly created these landscapes by classifying 10% of the cells as native habitat. We examined the effect of fragmentation by generating landscapes with variable clustering: from a single native-habitat fragment with 410 cells to 410 fragments with one cell each. For each landscape, we calculated extinctions using increasing sampling windows of size Ω (i.e. $\Omega = 1 \times 1$, $\Omega = 2 \times 2$, $\Omega = 4 \times 4$, etc) until the size of the lattice was reached (i.e. 64 × 64). We used the classic SAR, countryside SAR and the linear model to project the proportion of species extinctions in each sampling window k of size Ω in the landscape, $\varepsilon(a_k^{\Omega})$. Note that at the smallest sampling scale, sampling windows are only comprised of 1 cell ($\Omega = 1$), so we calculate $\varepsilon(a)$ for each of the cells (i.e. $\varepsilon(a_1^1)$, $\varepsilon(a_2^1)$, …, $\varepsilon(a_k^1)$) while at the largest sampling scale, the sampling window is comprised of all cells and $\varepsilon(a)$ is calculated for the entire landscape (i.e. $\varepsilon(a_1^{4096})$) (see Supplementary Fig. S2 for more details). Finally, at each sampling scale, the projections of each sampling window were averaged to obtain the overall proportion of species going extinct in the landscape (equation (5)). This procedure was repeated for each of the 1000 different spatially-explicit landscapes, and the resulting 1000 proportion of species extinctions curves for each model were averaged to produce Fig. 2.

Note that the linear model can be derived from equation (3) when $z = 1$,

$$\varepsilon(a) = \frac{a(1 - h_2)^1}{A} = \frac{a \cdot \sigma}{A}. \tag{6}$$

Therefore, using the linear model, $\overline{\varepsilon(\Omega)}$ is constant across scales but depends on the scale for the countryside and classic SAR models ($z < 1$).

We used the highest mean sensitivity for a human-modified habitat from Fig. 1, $\sigma_{P.crops} = 0.6$ ($h_1 = 0.01$, see Supplementary Note and Supplementary Table S2) and a value of $z = 0.20$ for the classic SAR and countryside SAR models, as it is an intermediate value of the wide range of z's reported in the literature for both plants and birds at this spatial scales[6,29,44,45]. In order to understand how the results from the three models change with different parameter values, we varied z from 0.1 to 0.3, σ_1 from 0 to 0.75, and the amount of native habitat left in the landscape from 10% to 90% (see Supplementary Fig. S3). We also explore in Supplementary Fig. S4, how the different models will behave in landscapes with different degrees of fragmentation (spatial clustering). These operations were carried out using RStudio 1.0.44[46], and the full R code is available on GitHub (https://github.com/ISMartinss/IEPAScaleHabitat).

Data accessibility. The dataset supporting this article have been uploaded as part of the supplementary material (Supplementary Table S1). Complete R code used for the simulations can be download here: https://github.com/ISMartinss/IEPAScaleHabitat.

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Author Contributions

I.S.M. and H.M.P. conceived and designed the study and wrote the paper. I.S.M. performed the data analysis.

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Chapter 4

Trends on higher land-use efficiency insufficient to mitigate impacts on nature from population and consumption growth

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Trends on higher land-use efficiency insufficient to mitigate impacts on nature from population and consumption growth

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Abstract

Biodiversity and ecosystem services losses driven by land use are expected to intensify as a growing and more affluent global population requires more agricultural and forestry products. In addition, teleconnections in the global economy lead to increasing remote environmental responsibility (Lenzen *et al.* 2012; Wilting *et al.* 2017). Here we provide an assessment of the impacts of the economy on biodiversity and carbon sequestration, and their dynamics in the last decade, by combining global biophysical and economic models (Chaudhary *et al.* 2015; Erb *et al.* 2016; Hudson *et al.* 2017; Stadler *et al.* 2018 p. 3). Between 2000 and 2011, despite gains in efficiency (i.e., impacts per unit GDP), overall population and economic growth resulted in increasing total impacts on biodiversity and carbon sequestration globally and in most world regions. The exceptions were North America and Western Europe, where the 2007-2008 financial crisis led to an actual reduction of forestry and agriculture impacts on nature. Biodiversity losses occurred predominantly in Central and Southern America, Africa and Asia with international trade as an important driver. In 2011, 33% of Central and Southern America and 26% of Africa's biodiversity impacts were driven by consumption in other world regions. In contrast, impacts on carbon sequestration were more homogenously distributed globally. Overall, cattle farming is the major driver of biodiversity loss, but oil seeds production showed the largest increases in biodiversity impacts during the analysed period. Forestry activities exerted the highest impact on carbon sequestration, much higher than any agricultural activity including deforestation, and also showed the largest growth in carbon impacts. Our results suggest that to address the biodiversity crisis, governments should take an equitable approach recognizing remote responsibility. Environmental policies should be tailored for each world region, promoting a shift of economic development towards activities with low biodiversity impacts and increase of consumer awareness to promote sustainable consumption, in addition they should take into account the importance of the Sustainable Development Goals (SDGs) in addressing population growth (Abel *et al.* 2016).

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Agriculture and forestry activities are major drivers of biodiversity loss and ecosystem degradation (MA 2005; Newbold *et al.* 2015; Venter *et al.* 2016). Population growth and economic development will continue to increase the demand for agricultural and forestry products, and shift consumption patterns towards products with higher overall environmental burdens (West *et al.* 2014; Venter *et al.* 2016). If unchecked, such strong demand-side drivers will cause higher pressures on biodiversity and ecosystems and put future well-being at risk (Cardinale *et al.* 2012). Ensuring sustainable production and consumption patterns, by decoupling economic growth from natural resource use and environmental impacts, is fundamental to sustainable development (UN 2015). However, teleconnections between world regions through international trade lead to an increasing disconnect between production and consumption, resulting in complex causal interrelationships, hampering straightforward analyses and resulting in governance challenges (Erb *et al.* 2009; Phalan *et al.* 2011; Lenzen *et al.* 2012; Laurance *et al.* 2014; Newbold *et al.* 2015; Verones *et al.* 2017; Wilting *et al.* 2017). In this study we systematically analyse the global impacts of agricultural and forestry activities on biodiversity and a key ecosystem service, the sequestration of atmospheric carbon in ecosystems, taking these complex production-consumption interlinkages into account. We quantify the magnitude and dynamics of these pressures from agriculture, forestry and the consumption of biomass products between 2000 and 2011 and analyse the role of underlying drivers such as population growth, economic development and technological progress.

Assessing the impacts of socioeconomic activities on biodiversity and ecosystem services is complex due to their multidimensional nature (Pereira *et al.* 2013; Reyers *et al.* 2017); this work covers one dimension of biodiversity and one ecosystem service. To assess the biodiversity impacts we focus on bird species richness, the species group best characterized in terms of responses to land-use activities (Newbold *et al.* 2015). We estimated, for each year, impending bird extinctions (i.e., number of species that would become extinct if land-use activities would be maintained in the long run) based on the number of endemic bird species in each biogeographical region (Methods, Supplementary Methods 1 and Supplementary Tables 1-2) and the amount and type of land being used for agriculture and forestry activities in each country or region (Methods and Extended Data Fig. 1). To assess the impacts on ecosystem services, we focused on net carbon sequestration, a key ecosystem service for climate change mitigation (Pan *et al.* 2011). We estimated the carbon sequestration lost each year, by calculating the potential additional carbon that would be sequestered if current land use ceased and natural vegetation were allowed to regrow

(Supplementary Tables 3-4). In order to quantify the consumption drivers we linked the two impact indicators to a multi-regional input-output (MRIO) model based on EXIOBASE 3, a new time series of MRIO tables (Methods; Stadler *et al.* 2018). Despite relying on established methodologies and openly available data it is worthwhile noting that a degree of uncertainty exists (Methods).

Globally, between 2000 and 2011 we found increasing impacts of agriculture and forestry on biodiversity and ecosystem services; the number of bird species with impending extinction due to land-use activities increased 7% (from 69 to 74), and the amount of carbon sequestration lost increased 6% (from 3.2GtC to 3.4GtC/year) (Supplementary Tables 1-4). As a comparison, 140 bird species were estimated to be lost since the beginning of the 16th century from all drivers combined (Ceballos *et al.* 2015), and in the period 2002 – 2010, global carbon emissions were estimated at 8 ± 2 GtC/year (30 ± 8 $GtCO_2$/year) (Blanco *et al.* 2014). Our estimates show that cattle farming had the highest impact on biodiversity, contributing to approximately 28% of total impending extinctions in 2011, mostly in Central and South America and in Africa (Fig. 1a). The production of oil seeds (including soy beans) was the activity with the highest contribution to the increase in impacts on biodiversity from 2000 to 2011 (Fig. 1b). The expansion of oil seeds production typically occurs at the expense of tropical forests (Vijay *et al.* 2016) rich in biodiversity. Forestry activities, i.e. the use of forests for timber and woodfuel extraction, had the highest impact on carbon sequestration, contributing approximately 30% of the total carbon sequestration lost (Fig. 1a), and contributed most to the increasing losses from 2000 to 2011, albeit a strong reduction of forestry impacts occurred in North America (Fig. 1b).

Increasing impacts have occurred despite improvement in land-use efficiency for biodiversity and carbon sequestration, i.e. biodiversity or carbon sequestration impacts per unit GDP (Fig. 2A and B). This happened because combined economic and population growth exceeded these efficiency gains from production both for biodiversity and carbon sequestration (Fig. 2a-b). We found consistent improvements in land-use efficiency in all world regions (Fig. 2c-d and Extended Data Fig. 2-3); in Africa, Asia and Pacific, Central and South America and Eastern Europe these were not sufficient to enable a reduction of the impacts caused by increased production. The overall decrease of the production impacts in Western Europe, Middle East and North America could indicate a decoupling of biodiversity and carbon sequestration impacts from economic growth. However, analysing decoupling trends only by assessing impacts from production activities taking place within a region might be misleading; a region may effectively import the environmental impacts from another region ("displacement effects") (Ward *et al.* 2016). Therefore, we used a MRIO model to assess the impacts from consumption activities.

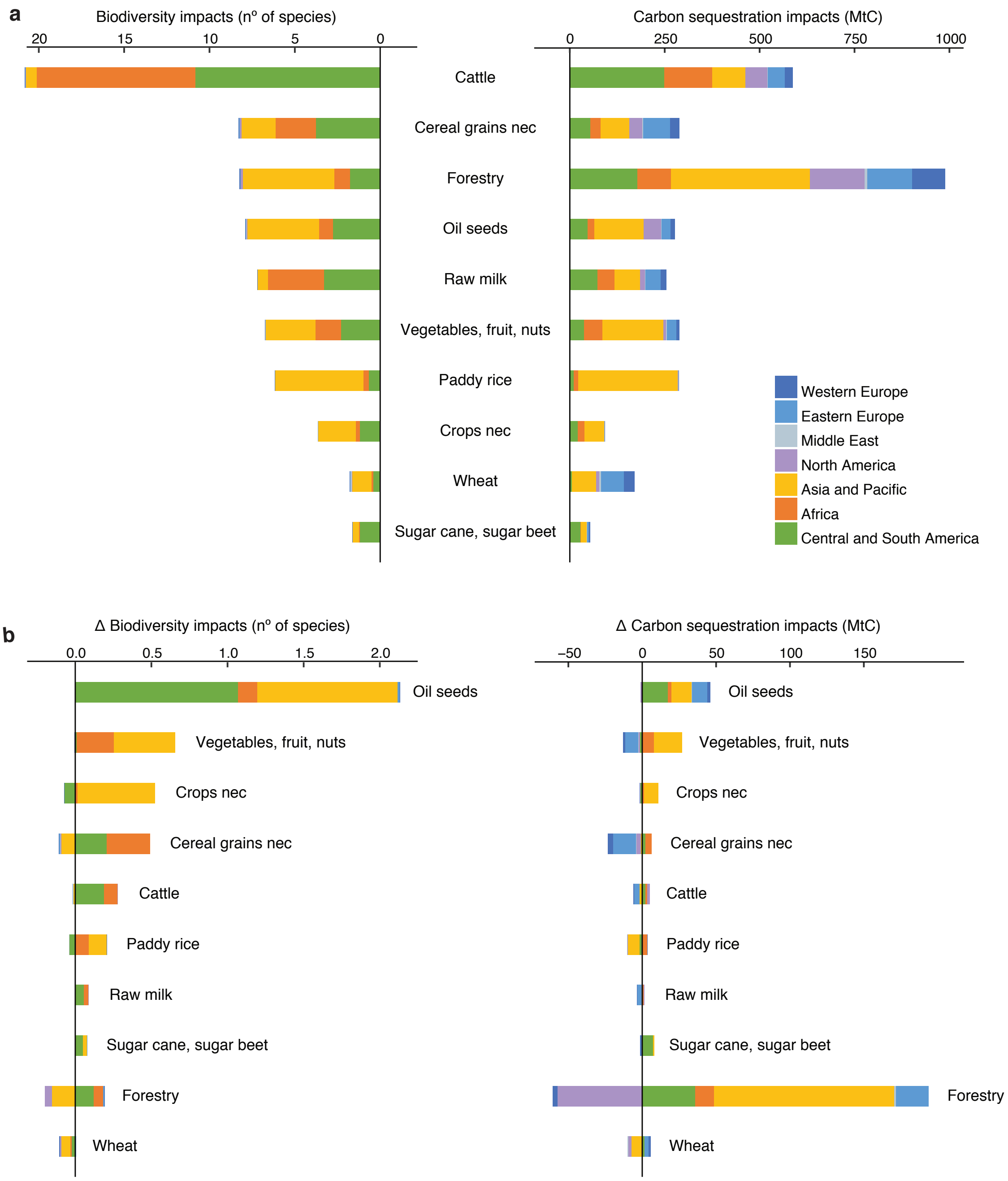

Figure 1 – Production impacts on biodiversity and carbon sequestration per economic sectors. a, Impacts in absolute terms for the year 2011; **b**, the difference between the impacts in 2011 and 2000. Negative values imply a decrease of their impacts by 2011. The left side are represents impending global bird extinctions (number of species) and on the right side carbon sequestration lost (MtC per year). Results are sorted by decreasing biodiversity impacts from production activities. The impacts associated with plant-based fibers, pigs, poultry and meat animals account for less than 1% each and are not represented. Nec stands for not elsewhere classified.

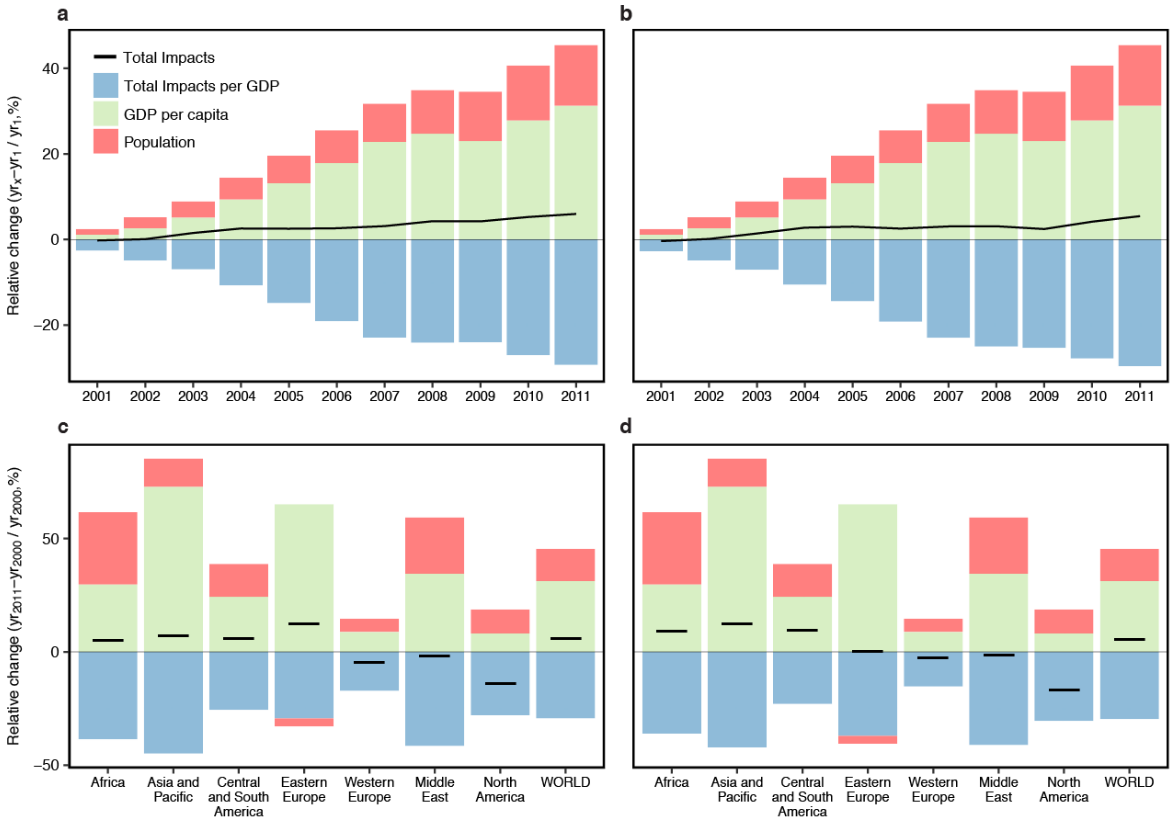

Figure 2 – Decomposition of changes in impacts of agriculture and forestry on biodiversity and carbon sequestration into the contribution of the changes in population, GDP per capita and impact per GDP. Biodiversity impacts are measured in terms of impending global bird extinctions, and ecosystem services impacts in terms of carbon sequestration lost. Impacts can be decomposed as (Methods): Δ Impacts = Δ Population × Δ GDP per capita (i.e., affluence) × Δ Impacts per GDP (i.e., land-use efficiency). Annual changes in production impacts relative to 2000 (Δ) at the global level for biodiversity (**a**) and ecosystem services (**b**), overall changes between 2000-2011 for different world regions for biodiversity (**c**) and ecosystem services (**d**).

The comparison between per capita impacts from a production and consumption perspective for the different world regions shows that the consumption patterns of an average citizen in North America, Western Europe, Eastern Europe and Middle East is driving biodiversity impacts elsewhere, i.e. consumption impacts are up to an order of magnitude greater than the production impacts for those regions, (Fig. 3a), and the same happens for carbon sequestration except for Eastern Europe (Fig. 3b). Furthermore, between 2000 and 2011, per capita consumption impacts decreased in North America, Western Europe, Africa and Central and South America (Fig. 3a-b). In contrast, in Eastern Europe, Asia and Pacific and Middle East consumption impacts per capita increased (Fig. 3a-b), reflecting the recent rapid economic expansion of these regions.

Our land-use efficiency analysis from both a production and consumption perspective shows that decoupling between economic growth and impacts occurs in Western Europe and North America, but not in the Middle East (Extended Data Fig. 2-3). While the decoupling in production impacts is expected, due to decreases in land use in both regions during the period analysed (Supplementary

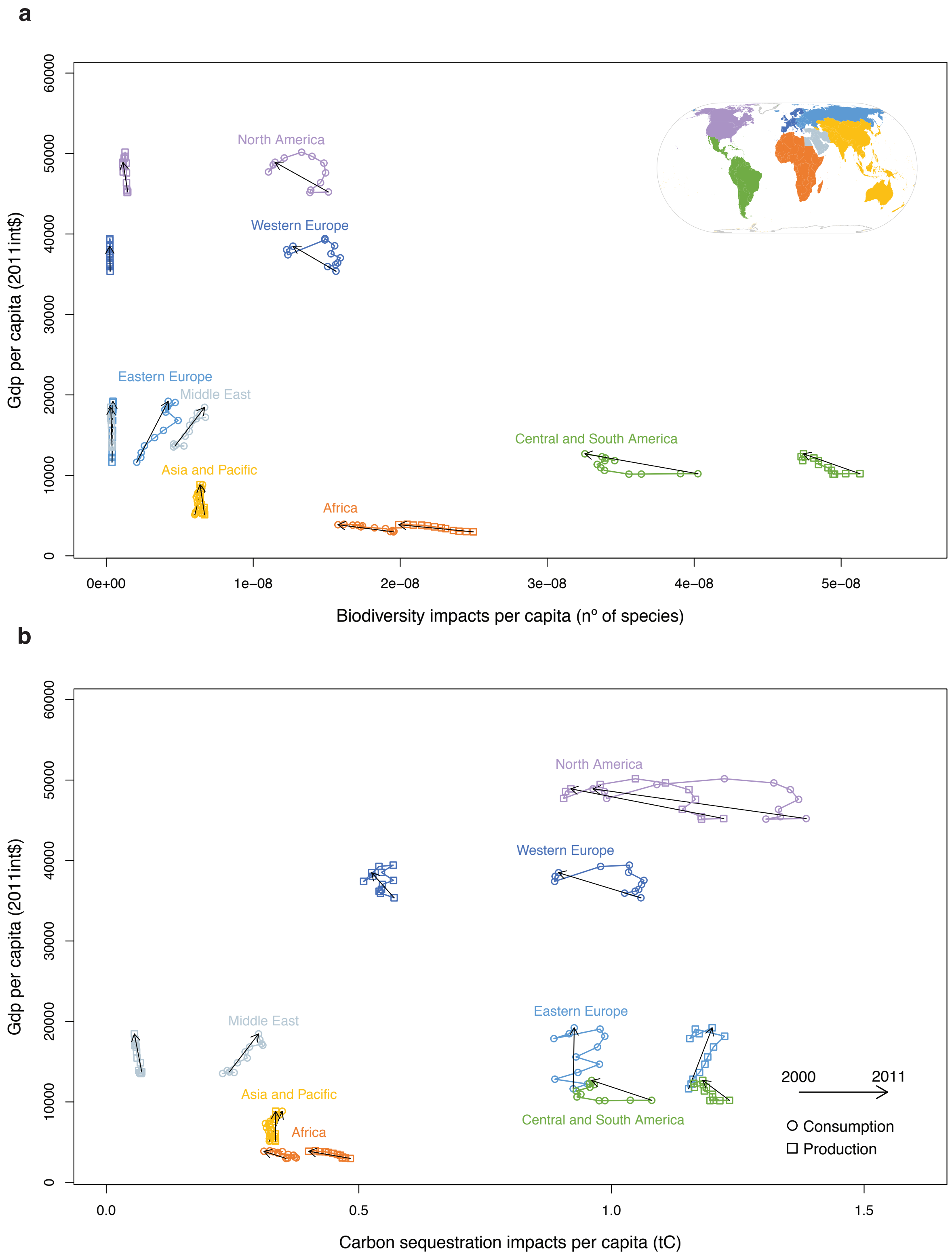

Figure 3- GDP per capita (in constant 2011 international$) and per capita impacts on biodiversity and carbon sequestration, per world region. Consumption and production impacts on biodiversity (**a**) as global impending bird extinctions (number of species per capita and year) and ecosystem services (**b**) as carbon sequestration lost (tC per capita and year).

Table 5), the decoupling in per capita consumption impacts is surprising and requires a reduction of consumption and/or an increase of the efficiency in the regions exporting to Western Europe and North America. In Western Europe, the consumption impacts on biodiversity and carbon sequestration decreased between 2007 and 2009 and in North America between 2006 and 2009. After 2009 there is again an increase in impacts for biodiversity, although by 2011 they were still below their 2001 levels. These results reflect the financial crisis, and consequent decrease in consumption that occurred in these regions. The decreases of the biodiversity impacts associated with agricultural activities are mainly due to decreases of food consumption in hotels and restaurants and a decrease in clothing purchases by consumers, both in Western Europe and North America (Extended Data Fig. 4a and Fig. 5a). These sectors are amongst those whose consumption was most affected during the financial crisis (Eurostat 2013). The decreases of the biodiversity and carbon sequestration impacts associated with forestry activities are mainly due to decreases in the manufacturing, construction and products of forestry sectors (Extended Data Fig. 4-5). Such findings reflect the reduction of the activity of the construction sector in both regions as a direct consequence of the financial crisis (Eurostat 2011; USDA 2014).

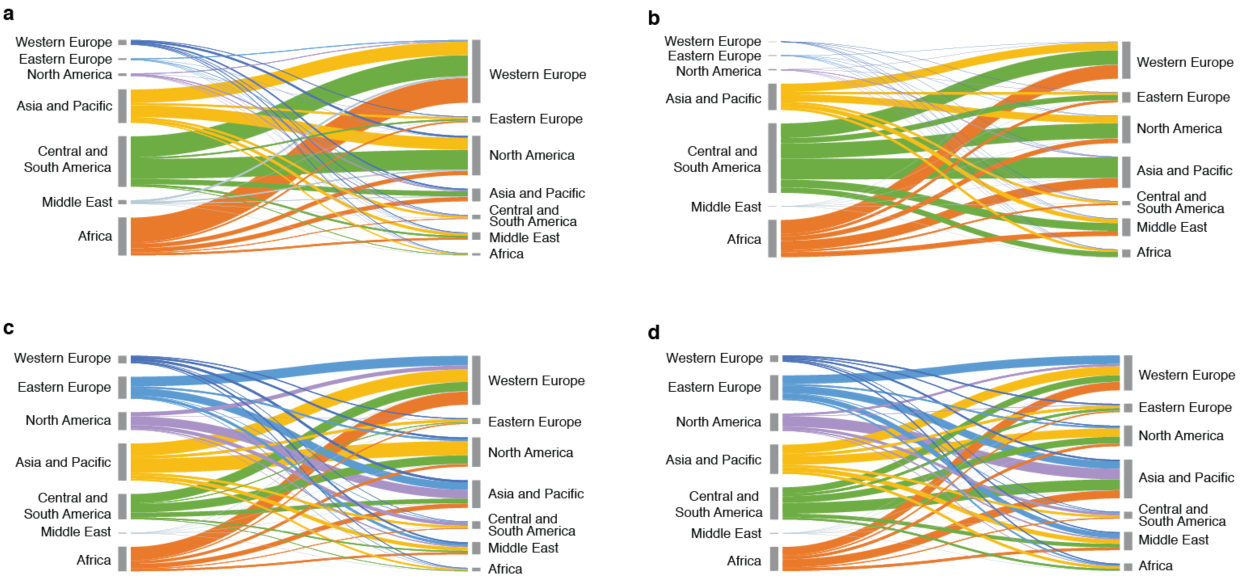

Figure 4 –Biodiversity (a,2000; b,2011) and carbon sequestration (c,2000; d,2011) impacts embodied in international trade. On the left is the region where the impacts occur and on the right is the region whose consumption is driving the impacts. The width of the flows represents the magnitude of the impacts. Exact values can be found in Extended Data Tables 1-2. Impacts arising from domestic production and consumption are not included in this figure. The visualized impacts represent 22%, 25%, 19% and 21% of the yearly global totals, respectively for biodiversity and carbon sequestration lost.

In any case, consumption based on internationally traded goods was driving 25% and 21% of the global impacts on biodiversity and carbon sequestration in 2011, representing a 3% and 1%, increase in relation to 2000, respectively (Fig. 3 and Extended Data Table 1-2). In 2000, Western Europe and North America were responsible for 69% and 58%, of the biodiversity and carbon sequestration impacts transferred through international trade; in 2011 these shares were reduced to 48% in the case of biodiversity impacts and 41% in the case of the carbon sequestration impacts (Fig. 4). In contrast the share of other regions were increasing fast: for example, Asia and Pacific drove 13% in 2000 and 23% in 2011 of the biodiversity impacts embodied in international trade; and 20% in 2000 and 29% in 2011 of the carbon sequestration impacts embodied in international trade (Fig. 3 and Extended Data Table 1-2).

Decoupling economic development and population growth from environmental impacts and natural resource use, e.g. via technological progress, is often seen as the solution to the current sustainability challenges (UNEP 2011; UN 2015). Our analysis highlights several intricacies related to such a perspective. In developed regions, a relative decoupling is observed, however it occurred mostly due to the financial crisis. In developed regions more than 90% of the biodiversity impacts from consumption as well as 40% of the carbon sequestration impacts from consumption, on average between 2000 and 2011, were outsourced (Fig. 3 and Extended Data Table 1-2). This is of particular concern in terms of global equity. For developing regions, continuous population growth and rapid economic development outweigh any efficiency increase. Our work suggests that the upcoming discussion of the parties to the Convention on Biological Diversity on the post-2020 biodiversity strategy should consider remote responsibility in an equitable way, and that policies need to be tailored to each region. Biodiversity issues in developing regions might co-benefit from the progress towards other SDG goals which might attenuate population growth (Abel *et al.* 2016). For developed regions and emerging economies, policies need to address the increasing teleconnection through consumption-based accounting to avoid any "biodiversity and ecosystem services impact leakage". Globally, we call for initiatives to change consumption patterns to mitigate further biodiversity and ecosystem services loss mainstreamed at the sectoral level.

Methods

The starting point for the quantification of the drivers of biodiversity and ecosystem services loss was a spatially-explicit land-use dataset, with information on 14 categories of land-use activities which cover all the agricultural and forestry production reported in authoritative international databases (FAOSTAT). This enabled determining the impacts to biodiversity and ecosystem services per km^2 of land-use activity (the so-called characterization factors). The characterization factors together with a time series of land-use data for 49 countries/world regions was used to determine the total impacts on biodiversity and ecosystem services, for the period 2000-2011. We referred to these as the supply side drivers of biodiversity and ecosystem services loss; these are the impacts driven by the production activities. To determine the consumption patterns driving biodiversity and ecosystem services loss we coupled the impacts from production activities to a multi-regional input-output model. We used the IPAT identity to distinguish the influence of population growth (P), economic development (A) and technological progress (T) on the evolution of the drivers of biodiversity loss and ecosystem degradation. The results were aggregated into 7 world regions, using EXIOBASE's world regions and the United Nations regional groups (UN 2014). In the following sections the methods are presented in detail.

Land use spatially explicit dataset

A spatially explicit land-use dataset for the year 2000, matching the sectoral resolution (for land-use activities) of the EXIOBASE dataset (see below Multi-regional input-output analysis and Supplementary Methods 2), was developed to assess the biodiversity impacts as well as carbon sequestration foregone due to agriculture and forestry activities (Stadler *et al.* 2018). The starting point of the assessment was the construction of a consistent and comprehensive set of layers at the spatial resolution of 5 arc minutes. We followed a previously published approach (Erb *et al.* 2007) and used a series of recent datasets for the year 2000 (restricted to this year by the availability of comprehensive cropland maps which currently are only available for the year 2000) to create the individual layers. A cropland layer (Ramankutty *et al.* 2008) was adjusted to reproduce newly published national statistics for cropland area for the year 2000 (based on the regular updates by FAO (FAOSTAT 2014) and data on cropland distribution (Ramankutty *et al.* 2008)). The cropland layer was split into nine sub-layers (corresponding to crop-categories in EXIOBASE) using the distribution of major crop groups (Monfreda *et al.* 2008): (a) paddy rice, (b) wheat, (c) cereals, grains nec (not elsewhere classified) (d) vegetables, fruit and nuts, (e) oil seeds, (f) sugar cane, sugar beet (g) plant-based fibres, (h) crops nec such as herbs and spicies and (i) fodder crops (Extended Data Fig. 1 and Supplementary Methods 2). Next, a recent global forest map was integrated into the dataset (Schepaschenko *et al.* 2015). This dataset is based on the integration of recent high resolution tree cover maps and a validation procedure through citizen science approaches, and applies a single definition of "forest" globally. Compared to FAO data this leads to a lower global forest cover estimate (32 Mkm^2 vs 42 Mkm^2). In cases, where the sum of the already allocated layers was >100%, the forest layer was capped. Information on intact forests (Potapov *et al.* 2017) was used to identify unused forests. The layer of permanent pastures was derived from (Ramankutty *et al.* 2008) and added to the grid, again capping the pasture layer at 100% land use coverage in each grid cell. This dataset is largely consistent with FAO statistics for permanent pastures, but uses national and subnational statistics and corrects the FAO data based on top-down considerations and plausibility checks. In consequence, the total sum for permanent pastures is 27Mkm^2 (in contrast to 35Mkm² in FAO). By taking non-productive areas (aboveground NPP below 20gC m^{-2} yr^{-1}) into account (Erb *et al.* 2007), permanent pasture land was further reduced to 23km^2. This reduction occurs mainly in dryland areas of Australia and central Asia and assumes that permanent pastures at a very low productivity do not contribute to grazing. Fodder crops were split into five separate layers (raw milk, cattle meat, pig meat, poultry and other meat), and permanent pastures into three layers (raw milk, cattle meat, other meat) (Müller *et al.* 2009), matching the available livestock sectors in EXIOBASE (Extended Data Fig. 1). The remaining areas can be considered under extensive, sporadic use, mainly for temporary livestock grazing and wood fuel collection. However, no biodiversity or ecosystem service impacts were allocated to them due to large uncertainties about the dimension and nature of the impacts of land use on these lands.

Correction of forest areas for quantification of biodiversity impacts

The approach described above gives an estimate of all forest areas not considered wilderness. In many contexts it will, however overestimate the amount of forests actively managed for forestry. To account for this, we used an alternative approach to estimate the area of managed forests: we first estimated the forest area that would have to be cleared to produce the harvest volumes (section Characterization factors for ecosystem services impacts for details on how biomass harvest data were assessed), assuming clear-cut regimes. To translate the estimates for harvest volumes into areas we assumed that biomass stocks at the time of harvest equal the average national potential biomass stocks (i.e., the stock that would prevail without land use but under current climatic conditions; from (Erb *et al.* 2016). In order to arrive at an estimate on areas managed for forestry, we multiply the amount of clear cut area with estimates of typical rotation times (Evans 2009; Penna 2010) (Supplementary Methods Table 3). Following this procedure yearly correction coefficients for each country were determined (Supplementary Methods Table 4).

In general, this estimate should give areas smaller or similar to the area calculated via the spatially explicit land-use datasets. In a few cases (Supplementary Methods Table 4) the numbers were higher, owing to uncertainties in all the data involved. To arrive at a conservative estimate, we use the smaller number of the two approaches as the area of managed forests considered in the biodiversity impact assessment, with the affinity parameter of the countryside species area relationship set for intensive forestry use (see Characterization factors for biodiversity impacts). To test the effect of this estimate we also computed the biodiversity impacts with the larger numbers and the affinity parameter of the countryside species area relationship set as the average value of the affinities for intensive and extensive forestry use (Extended Data Table 3). The results are reported in Supplementary Tables 6-7.

Characterization factors for biodiversity impacts

In order to quantify potential global bird species extinctions due to different land-use activities, we started by computing characterization factors (CFs) for each land-use activity (number of birds potentially extinct per km^2 of area used by land-use activity), based on the land-use dataset described in the previous section. To compute the extinctions associated to each individual land-use activity we used the countryside species-area relationship (cSAR) (Pereira and Daily 2006; Pereira *et al.* 2014). Species-area relationship models have been classically used to assess species extinctions after habitat loss, however this approach has a number of limitations. One issue is assuming that the number of species is mainly determined by habitat area, and that the habitat is uniform and continuous (Rybicki and Hanski 2013; Hanski *et al.* 2013). Another issue, that we believe to be even more prevalent, is that the classic SAR only captures the species richness response to changes in native habitat area, overlooking the diversity of species responses to changes in habitat composition. The countryside species-area relationship (Pereira and Daily 2006) describes the use of both human-modified and natural habitats by different functional species groups. Consider a completely natural landscape where habitat conversion takes place and only a single functional group of species is present. Then, according to the cSAR, the proportion of species remaining $\left(\frac{S^1}{S^0}\right)$ after habitat conversion is (Pereira *et al.* 2014)

$$\frac{S^1}{S^0} = \left(\frac{\sum_j^n h_j A_j^1}{h_1 A_1^0}\right)^z , \tag{1}$$

where *n* is the number of habitat types, h_j is the affinity of species to non-natural habitat *j* (hereafter called land-use activity *j*), h_1 is the affinity of species to the natural habitat, A_j is the area occupied by the different land-use activities *j*, A_1 the area of natural habitat before conversion takes place and *z* is a constant indicating the rate at which species richness increases with area. The superscript 0 indicates the natural state, and the superscript 1 indicates the modified state (i.e., after land-use change occurred). We used a value of *z* = 0.20, as it is an appropriate value for the spatial scales used in this work (biogeographical region) (Rosenzweig 1995; Storch *et al.* 2012). We assumed that species have maximum affinity for the natural habitat $(h_1 = 1)$ For human-modified habitats we calculated affinities as:

$$h_j = \left(1 - \sigma_j\right)^{1/z}, \tag{2}$$

where σ_j is the mean sensitivity of the species to each land-use activity *j* (Pereira *et al.* 2014). Sensitivity values (σ) were retrieved from previously published global databases (Sodhi *et al.* 2009; Chaudhary *et al.* 2015; Hudson *et al.* 2016) of studies of biodiversity responses to human-modified landscapes (Supplementary Methods 5). From these databases, we selected studies that provided data on bird species richness on both natural habitat and at least one human-modified habitat (i.e., land-use activity), as σ_j is the difference between the plot scale species richness found in the modified habitat of type *j* and the species richness in the native habitat (i.e., the proportion of species disappearing at the plot-scale in modified habitats), which led to a total of 319 pairwise comparisons. The data was subset into four land use classes based on the description of the habitat given in the source dataset: managed forest (extensive and intensive use), cropland, permanent crops and pastures; and two major biomes, tropical and temperate (Supplementary Methods 5). From these σ_j values and h_j were computed (see Supplementary Methods 5 and Extended Data Table 5). The correspondence between the habitats types used for the computation of the h_j values and the categories in our land-use dataset can be found in Supplementary Methods 2.

Using ArcGIS version 10.2 (ESRI 2009), we overlaid the land-use layers (see previous section for details on the spatially explicit land-use dataset), with a biogeographic region layer (Holt *et al.* 2013) to derive the current share of each of the fourteen land-use activities (13 agricultural types and forestry), A_j, per biogeographic region g, $A_{g,j}$. We used equation (1) to calculate the proportion of endemic species remaining after land-use change in each of the 19 biogeographical regions, with A_1^0 as the area of the biogeographic region *g*. Bird species' distribution maps (BirdLife International and NatureServe 2014) were used to derive the number of endemic species present in each of the biogeographic regions (S_g), 1295 endemic bird species were identify across all biogeographic regions (Supplementary Methods 1), which represents approximately 12% of the total number of bird species reported in (BirdLife International and NatureServe 2014). The total number of endemic species lost in each biogeographic region, ΔS_g, was calculated as:

$$\Delta S_g = \left(1 - \frac{S^1}{S^0}\right) \times S_g \,, \tag{3}$$

where S_g is the number of endemic species in a biogeographic region as determined through bird species distribution maps (BirdLife International and NatureServe 2014). Then, the total number of species lost per land-use activity *j* in each biogeographic region *g* was computed as follows,

$$\Delta S_{g,j} = \frac{w_j A_{g,j}}{\sum_j^n w_j \, A_{g,j}} \times \, \Delta S_g \, , \tag{4}$$

where $w_j = (1 - h_j)$ is a weight that reflects the impacts of the different land-use activities and *n* the number of land-use activities considered. For each biogeographic region *g*, the number of species lost due to each land-use activity *j* in each country *i* was then determined by taking into account the area of each land-use activity in each country that crosses the biogeographic region, $A_{g,i,j}$:

$$\Delta S_{g,i,j} = \Delta S_{g,j} \times \frac{A_{g,i,j}}{A_{g,j}} \, . \tag{5}$$

If a country contained more than one biogeographic region, the impacts across several regions were summed:

$$\Delta S_{i,j} = \sum_{g=1}^{G_i} \Delta S_{g,i,j} \, , \tag{6}$$

where G_i is the number of different biogeographic regions in country *i.* The biodiversity characterization factors, CFs, were then determined by dividing the $\Delta S_{i,j}$ by the area of each land-use activity *j* in each country *i*:

$$CF_{i,j} = \frac{\Delta S_{i,j}}{A_{i,j}} \, . \tag{7}$$

The biodiversity CFs (bird species potentially lost per km^2 of land use) were multiplied by the land-use data time series (see Multi-regional input-output analysis) to obtain the impending birds extinctions in every year. All calculations were performed using Python (Python Software Foundation 2010).

Previous studies (de Baan *et al.* 2013; Chaudhary *et al.* 2015) determined that the parameters associated with the responses of species to the environment were the ones contributing the most to the uncertainty of the characterization factors, due to the broad range of values spanning from positive to negative (i.e., from a detrimental effect to a beneficial one) and a heterogeneous distribution of the data in terms of taxa and biogeographical regions covered. In this study we focused on the birds group, the one which is best covered in terms of number of studies assessing their response to land-use change (Newbold *et al.* 2015). Despite limiting the uncertainty of our results by covering just one species group, it is still important to mention that the range of the values and the unbalanced geographical distribution (Extended Data Fig. 6) (for example, for temperate biogeographical regions there are 82 data points whereas for tropical there are 237 data points) are still important sources of uncertainty in the determination of the characterization factors. By using birds as a single functional group, we assume that all bird species respond equally to land use and habitat loss, also by considering broad geographic areas we ignore the effects of the particular characteristics of habitats (Hanski *et al.* 2013).

Characterization factors for carbon sequestration impacts

Ecosystems store large amounts of carbon in living biomass providing a crucial climate regulation service. Globally, the largest amounts of biomass carbon are stored in forest systems (Erb *et al.* 2018). Agricultural activities replace these natural ecosystems with agro-ecosystems (cropland and pasture) that provide higher amounts of biomass flows useful for society, but massively reduce vegetation carbon stocks. Forestry lowers carbon stocks through wood harvests, even if practiced sustainably, as forestry operations optimize the annual wood increment, which leads to lower carbon stocks compared to forests not under harvest regimes (Holtsmark 2011; Erb *et al.* 2018). When agricultural and forestry practices cease, systems can regenerate towards a more natural state. We estimated the carbon sequestration potential on land currently under use that would prevail in the absence of land use, the carbon sequestration potential lost. It is important to note that this potential is expressed as annual flow, but these flows cannot be expected continue infinite as carbon stocks in ecosystem without land use will saturate at some point. Thus, the indicator reflects short-to-medium term conditions only. This assumption, however, allows to unambiguously link carbon stock impacts and current land-use activities, irrespective of the long legacy effects of past land uses on carbon stocks (Houghton 2003; Kastner *et al.* 2011; Erb *et al.* 2018), and thus avoids incorrect attributions.

For agricultural land use, we assign the effect of land conversion (i.e., clearing of forests to agricultural fields) to the agricultural sectors in EXIOBASE (Supplementary Methods 2). We based our calculations on the land-use maps described in the land-use dataset section (see Land-use spatially explicit dataset**)** and combine them with a map of the carbon stocks in the potential natural vegetation (Erb *et al.* 2016) (i.e., the vegetation that would prevail without human land use). Due to large uncertainties relating to carbon stocks of non-forest ecosystems we perform the assessment only for agricultural land on potentially forested areas. These sites were identified by combining three biome maps (Ramankutty and Foley 1999; FAO 2001; Olson *et al.* 2001), and assuming potential forest cover where two of the three maps report a forest biome. Because of the omission of lands without potential forest cover, our estimate on the impact of agriculture on carbon stocks should be considered conservative.

We assume that in absence of agricultural land use, vegetation would grow back to 75% of the potential natural carbon stock value within 50 years (Houghton 2003). The calculations are performed on a global grid with a resolution of five arc minutes. The annual carbon sequestration lost (ΔC) in agricultural land-uses activities *j,* per grid cell *m* is calculated as:

$$\Delta C_{m,j} = \left(0.75 \times \frac{C_m^o}{50}\right) \times A_{m,j}, \tag{8}$$

where C_m^o is the potential biomass carbon stock per unit area in the grid cell *m* and $A_{m,j}$ is the area of agricultural land-use activity *j* in the grid cell m. In equation (8) we implicitly assume that the carbon stock of agricultural land is negligible compared with the potential carbon stock. To link the indicator to the multi-regional input-output model an indicator per country *i* and land-use activity *j* was computed:

$$\Delta C_{i,j} = \sum_{m=1}^{M_i} \Delta C_{m,j}, \tag{9}$$

where $\Delta C_{i,j}$ represents the amount of carbon sequestration lost due to each land-use activity *j* in each country *i,* and M_i is the number of grid cells per country *i.*

For forestry a different approach was required to account for the effect of forest management on carbon stocks. The difference between potential carbon stocks and current stocks is not a good proxy for this effect, as this difference is largely influenced by land-use histories and not solely by present use. To unambiguously account for the effect of forestry on carbon socks, we focus on wood harvest, the main purpose of forestry activities. We assume that, at the national level, annual carbon sequestration lost due to forestry equals the biomass removed by wood harvest (industrial roundwood and fuelwood) activities in a given year (Kastner *et al.* 2011). For this we convert annual wood harvest quantities from FAOSTAT (2014) into carbon, taking into account bark and other biomass destroyed in the harvest process, but not removed from the forests, correcting for the fact that part of this biomass was foliage and would not have contributed to long term carbon sequestration (factors from Krausmann *et al.* (2008)). Part of the harvested wood is stored in long lived products, representing a form of carbon sequestration. We account for this, by deducting amount of industrial roundwood that ends up in such products (about 20% of harvested industrial roundwood globally, based on Lauk *et al.* (2012)). The national level data for annual carbon sequestration lost due to forestry, $\Delta C_{i,forestry}$, were aggregated where necessary to match EXIOBASE's regional resolution (Supplementary Methods 6) .This approach disregards ecosystem effects such as compensatory growth and thus only holds for a short term perspective, but gives an indication on how forestry practices currently lower the potential sink function of biomass in ecosystems (Holtsmark 2011; Pingoud *et al.* 2018; Schlesinger 2018).

The ecosystem services characterization factors, CFs, were then determined by dividing the $\Delta C_{i,j}$ by the area of each land-use activity *j* in each country *i*:

$$CF_{i,j} = \frac{\Delta C_{i,j}}{A_{i,j}} \, . \tag{10}$$

Similarly to the biodiversity CFs, the ecosystem services CFs (carbon sequestration lost per km^2 of land use) were multiplied by the land-use data time series (see Multi-regional input-output analysis) to obtain carbon sequestration lost in every year.

Multi-regional input-output analysis

Multi-regional input-output (MRIO) analysis has been increasingly used to identify the consumption drivers of environmental impacts. Environmental impacts analysed within an MRIO framework include emissions of pollutants, appropriation of natural resources and loss of biodiversity (Davis and Caldeira 2010; Lenzen *et al.* 2012; Wiedmann *et al.* 2015). Environmentally-extended MRIO (EEMRIO) models are particularly suited to track the spatial disconnection between environmental pressures from production processes and the consumption drivers behind them as they cover the world economy and the international trade relations between different countries and sectors. In this work we followed the standard Leontief model to compute the biodiversity and ecosystem services impacts from consumption activities. The standard environmentally extended Leontief pull model is formulated as follows (Kitzes 2013):

$$E = f(I - A)^{-1}Y \tag{11}$$

Where (for *i* countries and *m* economic sectors):

- *E* is the (1 x *i*) matrix of environmental impacts associated with final demand of each country.
- *f* is a (1 x *i.m*) direct intensity vector, which gives the environmental pressures (biodiversity and ecosystem services losses) associated with 1€ of production of the economic sectors. Since in this work we quantified the biodiversity and ecosystem services losses associated with land-use activities this vector will be a sparse vector only populated in the entries for

land-use activities. The biodiversity and ecosystem services losses are calculated by multiplying the previously determined characterization factors (CFs) by the amount of land used in each year by a given land-use activity. The amount of annual land used was extracted from the MRIO database used (see below for more details).

- A is the ($i.m$ x $i.m$) matrix of technical coefficients, which gives the amount of inputs that are required to produce 1€ of production.
- Y is the ($i.m$ x i) matrix of final demand in monetary terms.
- I is the ($i.m$ x $i.m$) identity matrix.
- The matrix inversion is represented by the exponent $^{-1}$.

More details on the calculations underlying environmental input-output analysis can be found elsewhere (Miller and Bair 2009; Kanemoto *et al.* 2012; Wilting *et al.* 2017).

The MRIO database used in this work was EXIOBASE 3; this database provides a harmonized time series of MRIO tables and environmental extensions ranging from 1995 to 2011 (Stadler *et al.* 2018), sectoral disaggregation of 200 products and 49 regions/countries (Supplementary Methods 6 and 7). Particular important to this work and for the time-series calculation of the biodiversity and ecosystem services are the land-use accounts, developed consistently to the spatial explicitly land-use data set (Stadler *et al.* 2018).

MRIO models are top-down models that assume a linear relationship between a unit of demand, and the production (and, in this case) land use required to produce goods and services along the supply chain. Accuracy of MRIO analysis is estimated to be in the order of 10-20% at the national level (Lenzen *et al.* 2010; Moran and Wood 2014), given a consistent coverage of the account for the environmental pressure (in this case, land use). High sector detail helps to reduce this uncertainty (Lenzen 2011; de Koning *et al.* 2015), and the EXIOBASE MRIO model provides the highest harmonized sector detail available (Wood *et al.* 2014). Regional aggregation affects results in a similar way to product aggregation (Stadler *et al.* 2014). Whilst many comparative MRIO studies find quantitative differences between databases, they also point to robust trends for consumption based accounts observed in all EE MRIO studies such that qualitative conclusions from the quantitative data are reliable (Lenzen *et al.* 2010; Lenzen 2011; Moran and Wood 2014; Stadler *et al.* 2014; Steen-Olsen *et al.* 2014; Wood *et al.* 2014; de Koning *et al.* 2015; Owen *et al.* 2016).

IPAT Identity

We used the IPAT identity (Ehrlich and Holdren 1971) to distinguish the influence of population growth (P), economic development (A) and technological progress (T) on the evolution of the drivers of biodiversity loss and ecosystem degradation through time:

$$\mathrm{I} = \mathrm{P} \times \frac{I}{A} \times \frac{A}{P} \tag{13}$$

I refers to impacts (on biodiversity and ecosystem services), in this work the absolute amount of impacts was determined from a supply side perspective, by multiplying the CFs with land-use data, and from a demand side perspective through multi-regional input-output analysis. P refers to population. A refers to affluence measured as Gross Domestic Product (GDP). $\mathrm{I}/_{A}$ is a metric of technological progress and it measures the impacts per unit of GDP. The higher the value less efficient is the economic as more impacts are generated per unit of GDP. $\mathrm{A}/_{P}$ is the metric of affluence in per capita terms. Population data was retrieved from (World Bank 2015a) and GDP data was collected in 2011 international dollars (corrected for purchasing power parity) from World Bank (2015b).

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Chapter 5

Winners and losers: How different pathways to a sustainable future affects species communities

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Winners and losers: How different pathways to a sustainable future affects species communities

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Abstract

Land use change is currently the main driver of biodiversity loss. Projections of land use change are often used as a toll to estimate potential impacts on biodiversity of future pathways of human development. However, such analysis frequently neglect that species often face habitat change instead of habitat loss, and that not all species respond equally to habitat change. Our aim was to estimate changes in biodiversity, within species functional groups, resulting from projected land use changes following two distinct sustainable transition scenarios, compared to a business-as-usual scenario. Using Portugal as a case study, we produced spatially-explicit projections of land use change based on two alternative descriptions of sustainable future pathways. A Pathway A, where sustainability is achieved via large-scale technological improvements and a Pathway B where sustainability is achieved via societal changes such as changes in behaviour and consumption patterns. Then, we used the countryside species-area relationship (cSAR) model to assess the resulting changes in species richness projected to occur by 2050 in each of the scenarios, using birds as an indicator taxa. By 2050, alpha and gamma bird species richness was projected to increase, relative to 2010, in all scenarios of land use change. However, different pathways favored different species groups, and presented strong regional differences. In the technological improvement pathway, loss of agricultural areas led to an increase in both natural and extensive forest areas. On this pathway the increase of total species richness was led by an increase of forest species, at the cost of farmland biodiversity, with the latter projected to decrease below the values estimated for the business-as-usual scenario. By contrast on the societal change pathway, changes in total species richness were mostly driven by an increase of farmland species, as extensive agricultural areas were projected to increase, particularly in central and southeast Portugal. Here, we show that whichever pathway is chosen to achieve a sustainable future it will have important and differential impacts on biodiversity, and result in very different species composition. Furthermore, such impacts can change depending on the local social-economic context, thus we suggest that different strategies should be pursued in unison to better preserve biodiversity at larger scales.

Introduction

Biodiversity has been declining steadily over the last decades (Pimm *et al.* 2014). While biodiversity loss has multiple drivers, habitat destruction via land use change is considered to be a primary driver of biodiversity change (Pereira *et al.* 2012). In the future, the pressure on land is likely to increase, as global human population is expected to grow from around 7 billion in 2010 to 9 billion by 2050, thus increasing food consumption by 1.7 times and wood consumption by 1.3 times (van Vuuren *et al.* 2012). Such increase in consumption is likely to lead to further habitat conversion and associated biodiversity loss. However, there is uncertainty as to how the increasing demand for goods will affect land use dynamics in the future.

In order to reach the conservation targets set to 2020 by the Convention on Biological Diversity (CBD 2011) and the UN sustainable development goals for 2030 (UN 2015), policy- and decision-makers need tools to evaluate the effects of possible management actions and policy measures under future environmental conditions (Pereira *et al.* 2010; Kok *et al.* 2017; Rosa *et al.* 2017). Scenario analysis of alternative plausible futures (i.e., pathways of events under a set of key assumptions) is often used as a tool to explore and evaluate the extensive uncertainties associated with the future (van Vuuren *et al.* 2012) . However, most of the scenarios that assess the impact of land use change on biodiversity are based on integrated assessment models developed by the climate science community (Jantz *et al.* 2015). These models focus on the impact of land use on climate, and tend to capture only the conversion between broad land use classes (van Vuuren *et al.* 2012; Titeux *et al.* 2016). Furthermore, most scenarios of biodiversity loss neglect the ability of species to disperse or adapt to changing environments, and simplistically assume that natural habitat modified by human activities cannot harbour native biodiversity (Pereira and Daily 2006a; Thuiller *et al.* 2013). In reality, the impact of land use on biodiversity is complex. For instance, the impact not only depends on the amount and type of land used, but also on its spatial distribution and intensity (Chaudhary *et al.* 2015). While some species are highly sensitive to habitat loss and only occur in native habitats, others show partial or total tolerance to human-modified habitats, with some species even benefiting from the conditions found in human-modified habitats (Martins *et al.* 2014; Newbold *et al.* 2015; Martins and Pereira 2017). Consequently, species responses to land use change may vary considerably between and within species groups depending on whether the change in habitat actually results in habitat loss. For example, agricultural practices are often responsible for the destruction and fragmentation of native habitats, affecting local biodiversity negatively (Poschlod *et al.* 2005).

It has been argued that the current trend of farmland abandonment in Europe (Schultz *et al.* 2015; Levers *et al.* 2015) should be welcomed by the conservation community as an opportunity to improve habitat condition for species (Queiroz *et al.* 2014) and as an opportunity for rewilding (Navarro and Pereira 2012). However, the relationship between farmland abandonment and biodiversity response is not straightforward (Matson and Vitousek 2006; Vandermeer and Perfecto 2007; Navarro and Pereira 2012). Studies have shown that the decline of traditional agricultural practices often have negative effects on local biodiversity, especially on farmland birds (Moreira *et al.* 2012). More broadly, these considerations also feed into the discussion around the "land sparing versus land sharing" framework for nature conservation (Phalan *et al.* 2011). Specifically, "land sparing" approaches consider that conservation and food production should be spatially separated in the landscape, with intensive high-yield agriculture on some areas and protected or restored natural areas on other areas (Merckx and Pereira 2015; Phalan *et al.* 2016), while "land sharing" relies on the assumption that conservation and food production can be achieved within the same multifunctional landscapes (Green *et al.* 2005).

There is an urgent need to assess with greater accuracy the responses of biodiversity to land use change under different sets of future socioeconomic developments, so as to integrate human development and nature stewardship in a sustainable way (Rosa *et al.* 2017). Here, we develop a framework based on the countryside SAR model (Pereira and Daily 2006a) to project biodiversity changes, not only from the loss of native habitat but also from an increase in modified habitats, such as farmland areas. In addition, by considering the differential use of habitat by different species groups, the countryside SAR model allows a more precise detection of community responses to land use change. Using Portugal as a case study, we aim to assess the response of biodiversity to three distinct land use change scenarios, and how three functional species groups (i.e., forest species, farmland species and species with affinity for other natural habitats) will perceive the habitat changes projected in each of these scenarios. We also compare species responses, between and within these species groups, to the alternative future human-modified landscapes.

Methods

The Pathways Scenarios

Our analysis was based on two distinct sustainable transition scenarios developed by the EU FP7 project PATHWAYS (www.pathways-project.eu). The project aimed at exploring the possibilities for transitions into a low-carbon, sustainable Europe. These scenarios were designed to achieve a broad set of sustainable development objectives based on existing international agreements. The first scenario, hereafter “Pathway A”, is a technical component substitution scenario and assumes that targets for sustainability are achieved via large-scale technological improvements, without a full reordering of existing societal structures. In Pathway A, better yields and the development of precision farming (i.e., high efficient agriculture) allow for the intensification of agriculture in productive areas that are already being cultivated. As a result, there is an increase in the abandonment of less productive and marginal farmlands. Management practices that maintain early successional habitats increase natural areas, while more areas transition to extensive forest. This pathway would lead to a “land sparing” approach with food and timber production focused on intensive agricultural and forestry areas, and with increased area for nature conservation and rewilding on abandoned farmland.

The second scenario, hereafter “Pathway B”, is oriented towards a stronger societal transformation. This scenario entails a shift to a new socio-technical system driven by societal changes impacting/influencing behavior and consumption patterns (e.g., lower meat and dairy consumption, reduction of waste). Moreover, in this scenario agriculture and nature protection are combined creating multifunctional landscapes, with ecological reserves in productive areas. Such changes would lead to an extensification of the agricultural landscape. The co-occurrence of environmentally-friendly agricultural practices and nature conservation in this scenario promotes a “land sharing” approach.

Both Pathways were contrasted with a business-as-usual scenario, hereafter “Pathway 0” in which no new policies are introduced in order to specifically achieve sustainable developments targets, i.e., the historical trends of land use change were maintained into the future. For a full description of the assumptions of each Pathway see van Sluisveld *et al.* (2016).

The case study: Portugal

We investigated how biodiversity would respond to projected land use change in Portugal up to 2050 in each of the scenarios (i.e., Pathways 0, A and B). Portugal is an interesting case to study due to its strong socio-economic heterogeneity and dynamic history of land use change. Agriculture represents more than a third of the Portuguese national territory (MAMAOT 2013a, b). However, since the 1960s, and due to a marked rural exodus, agricultural lands in the north of Portugal have been systematically abandoned, leaving large areas to natural succession. On the other hand, and after the 2nd half of the 20th century, agriculture practices in Portugal intensified, with less productive agriculture areas often converted into extensive pastures, particularly in the south of the country. In contrast, the area occupied by the traditional Montado agro-forestry system remained relatively unchanged, due to its strong economic and cultural value (Pereira *et al.* 2009; INE 2011; Jones 2011; Levers *et al.* 2015). In the last century, the increase in Portuguese forest was marked by high human intervention, with forestry now representing about 36% of the Portuguese national territory. In the first half of the century, afforestation mostly happened as an effort to recuperate eroded soil, where large areas of maritime pine (*Pinus pinaster*) were planted. However, after 1970s, and in response to an increase in demand from the logging and paper industry, large areas were converted into eucalyptus (*Eucalyptus globulus*) plantations, often at the expense of maritime pine (MAMAOT 2013a; Reboredo and Pais 2014), drastically changing the Portuguese forest composition (Jones 2011; Gonçalves and Pereira 2015). Moreover, agro-forestry and forestry systems produce commodities such as cork and paper, which taken together generate a revenue that comprise 2% of the annual GDP and 10% of the national exports (ICNF 2017). These dynamics (e.g., changes in forest cover, agricultural abandonment and intensification of the agricultural land) have also shaped biodiversity dynamics (Pereira *et al.* 2009). For instance, scrub encroachment associated with agricultural abandonment and forest plantation in agricultural land has been linked to declines in bird communities, particularly open farmland species (Moreira *et al.* 2012). While the increase in semi-natural vegetation resulting from agricultural abandonment, has favored the recovery of species previously impacted by the agriculture expansion (Pereira *et al.* 2009).

Projecting future land use change under each Pathway

We have characterized the land uses in Portugal into three use regimes: agriculture, forestry, and natural areas. For this analysis, we further divided agriculture and forestry into intensive and extensive use of the land, resulting in five land use classes: intensive agriculture, intensive forest, extensive agriculture, extensive forest and other natural (i.e., natural areas minus forests or agriculture areas). Finally, given the recent slowdown in urban area expansion and the fact that these areas only represent 4% of the national territory (Caetano *et al.* 2017), they were assumed to remain constant and thus excluded from the list of relevant land-use classes in this study.

Data sources

We projected future changes in land use until the year 2050, using a combination of datasets and tools, namely the CORINE Land Cover Map of 2012 (at 100 m resolution, EEA 2016), the distribution map of forest tree species in Portugal (derived from the 2010 national forest inventory, Rosa et al. 2011), national statistics on agricultural areas (INE 2011) and the Pathways storylines (see section 2.1). First, we created the baseline land use map of 2010 by combining CORINE Land Cover data for Portugal in 2012 with the forest species map produced by Rosa *et al.* (2011). We then reclassified

CORINE’s legend into the five land-use classes (Table S1). Afterwards, using historical national statistics (1990-2010) from the National Forest Inventory (MAMAOT 2013a) and the national Agricultural Census (INE 2011), we determined the historical trends (i.e., % of land being converted), which were then used and adapted to each scenario in order to produce the land use maps for the year 2050 for Pathway 0, and the two sustainable pathways, respectively (supplementary methods S1 for details).

Land use transitions in Portugal under each Pathway

For the business-as-usual scenario (i.e., Pathway 0) we assumed that future land use change will continue the observed trends of the last 20 years (Table SM1, supplementary methods S1 for details). Pathways A and B both have the same overall aim of achieving the goal of a sustainable society by 2050). However they differ on the means to achieve such target, which has implications on the land use transitions expected by 2050. For these two pathways, we tailored the historical trends for the period 2010-2050 in order to fit the storylines described above (section 2.1). In particular, for Pathway A, both intensive agriculture and intensive forest were locked, meaning that the proportion of the area that they occupy in the country was not assumed to change from 2010 to 2050 (Table SM2, supplementary methods S1). Given the focus on technological improvements and the ‘land sparing’ dimension of Pathway A we assumed a doubling of the rate of loss in extensive agriculture compared to the historical trend, as we expect the abandonment of less productive and marginal agriculture areas, but maintained the transitions rate to extensive forest and to other natural areas. In Pathway B, the area occupied by intensive forest was locked and we assumed a 50% reduction in the area of intensive agriculture by 2050 (Table SM3, supplementary methods S1). This area would transition completely to extensive agriculture, representing extensification of the landscape and increase of multifunctionality (i.e., ‘land sharing’ dimension of Pathway B). We also locked the transition between extensive agriculture and extensive forest (e.g., no new pine plantation), and assumed a 50% reduction in the rate of extensive forest loss due to fire, since landscapes are expected to become more fire resilient (Gonçalves and Pereira 2015). Finally, and as a result of a projected increase in management to maintain natural areas, we assumed for both Pathways A and B a decrease in the rate of natural succession, compared to the business-as-usual scenario.

Mapping future land use change under each Pathway

Land use change is not uniformly distributed across Portugal, therefore, we used a spatially-explicit model to allocate the projected changes by 2050, assuming that transitions to a new land use class (e.g., from intensive agriculture to extensive agriculture) would be more likely to occur closer to existing areas of the same land use (i.e., extensive agriculture), thus expanding existing patches, rather than creating new ones. To do so, we calculate the Euclidean distance of each pixel to each of the five land use classes in 2010, and then iteratively selected the pixels to transition based on the minimum distance to a given land use. As a result, we produced three new land use maps for Portugal, each representing a different vision for 2050 (Pathways 0, A and B).

Effects of land use change on biodiversity

Once the land use maps for 2050 were created, we used the countryside species-area relationship (cSAR) (Pereira and Daily 2006; Martins and Pereira 2017) to assess the response of species richness to the projected changes in land use in Pathways 0, A and B. Built on the power model ($S=cA^z$), the cSAR overcomes the simplistic assumption of the classic SAR that when all habitat is converted to human-modified habitats all species go extinct, by introducing a parameter (h_{ij}) reflecting the habitat affinity of a functional species group *i* to a human-modified habitat type *j*. The cSAR approach accounts for the persistence of species in modified habitat and captures the response of species richness to changes in both habitat area and composition. Therefore, after habitat conversion, the proportion of species in a functional group remaining in the landscape will depend on the level of affinity of that species group to the human-modified habitats. In the countryside SAR the richness of each functional species group *i*, S_i, is given by

$$S_i = c_i \left(\sum_{j=1}^{n} h_{ij} A_j \right)^z , \tag{1}$$

where *n* is the number of modified habitats types, h_{ij} is the affinity of species group *i* to habitat *j* and A_j is the area cover by habitat *j*. The parameters *c* and *z* are constants that depend on the taxonomic group and sampling scheme respectively, and are species group dependent.

We used equation (1) to calculate alpha (local; 10 km x 10 km UTM cells) and gamma (national) species richness of three different bird functional groups: forest species, farmland species and “other species” (i.e., species with affinity for other natural habitats, such as shrubland or grasslands) for the baseline and each of the three scenarios considered. The different functional group-specific parameters (i.e., c_i, z_i and h_{ij}, the habitat affinities) were derived from Martins *et al.* (2014), where the differential use of natural and human-modified habitats by different bird species groups in Portugal was assessed (Table S2). However, the authors did not assess species responses to intensively used habitats, subsequently the affinities listed by Martins *et al.* (2014) were assumed to be for extensive landscapes. To calculate the intensive land use classes we assumed that species affinities reported by Martins *et al.* (2014) would decrease proportionally to the decrease in species observed in local studies where intensive landscapes were sampled (see supplementary methods S2 for details). The area of each modified habitat in each cell of the land use maps (see section 2.3) was calculated for the different land use maps using ArcGIS 10.2 (ESRI 2014), and used as an input in the cSAR. The total number of species in the landscape, S_i, was then given by the sum of species in each group ($S = \sum_{i=1}^{m} S_i$,where m is the number of species groups). Finally, we assessed the differences in species richness between the baseline (i.e., 2010) and the three projected Pathways for each functional species group as well as for the total species richness.

Results

Land use change

We estimated that in the baseline (i.e., 2010) 60.9% of Portugal's territory (excluding urban areas) was under extensive use, while 20.8% of the area was being used intensively. The remaining area (18.3%) corresponded to natural areas that were not forests or agriculture areas and were not under any use (i.e., other natural, Table 1). By 2050, and in the business-as-usual scenario, we projected an increase in both the area of intensive and extensive forest, in the central and north-northeast part of Portugal (Fig. 1, Table 1). Forest areas under intensive use are projected to increase as a consequence of the expansion of eucalyptus plantations, while the projected increase of extensive forest areas is mostly due to natural succession on abandoned farmland (see Table SM1 and supplementary methods S1 for details).

Table 1. Proportions (in %) occupied by the different land use classes in 2010 and by 2050 under the assumed scenarios (Pathway 0, A and B). Future trends of land-use change (in %) for the period 2010-2050 (in parentheses) under each scenarios are also shown.

	Actual	Projected					
	2010	2050 (2010-2050)					
		Pathway 0		*Pathway A*		*Pathway B*	
Total area (%)							
Extensive Forest	26.46	32.87	(+24.24)	36.50	(+37.95)	30.36	(+14.75)
Intensive Forest	10.94	16.95	(+54.95)	10.94	(0)	10.94	(0)
Extensive Agriculture	34.47	29.41	(-14.67)	22.75	(-34)	38.42	(+11.47)
Intensive Agriculture	9.83	9.11	(-7.37)	9.83	(0)	4.92	(-50)
Other Natural	18.30	11.65	(-36.31)	19.98	(+9.71)	15.36	(-16.07)

Areas devoted to extensive agricultural production are projected to decrease by 14.7% (i.e., the overall area of agriculture changed from 34.5% in 2010 to 29.4% in 2050, Table 1), as observed in the historical trends. In the southeast and northeast part of Portugal, such a decrease is projected to be a result of land abandonment (i.e., conversion to other natural areas) and intensification of the agricultural areas, while in the center and northwest of the country agriculture areas are mostly converted to extensive forest areas (e.g., new pine plantations). By 2050, more natural areas are being converted to forest than being created by agricultural abandonment or fire events, leading to an overall reduction of the country's other natural areas (11.7% in 2050 *vs* 18.3% in 2010, Table 1 and Table SM1).

Given the focus on technological improvements and the 'land sparing' dimension of Pathway A, intensive agricultural areas remain constant, but a strong reduction in the area devoted to extensive agriculture in the north- northeast of Portugal is projected. From 34.5% in 2010, extensive agriculture reduces to 22.8% in 2050 as a result of agricultural land abandonment, and conversion to extensive forest (e.g., new pine plantations, see Table 1 and Table SM2 for details). Moreover, in Pathway A we projected a significant increase in extensive forest and other natural areas, which together by 2050 would represent 56.5% of the non-urban area of the country, compared to 45.7% in Pathway B.

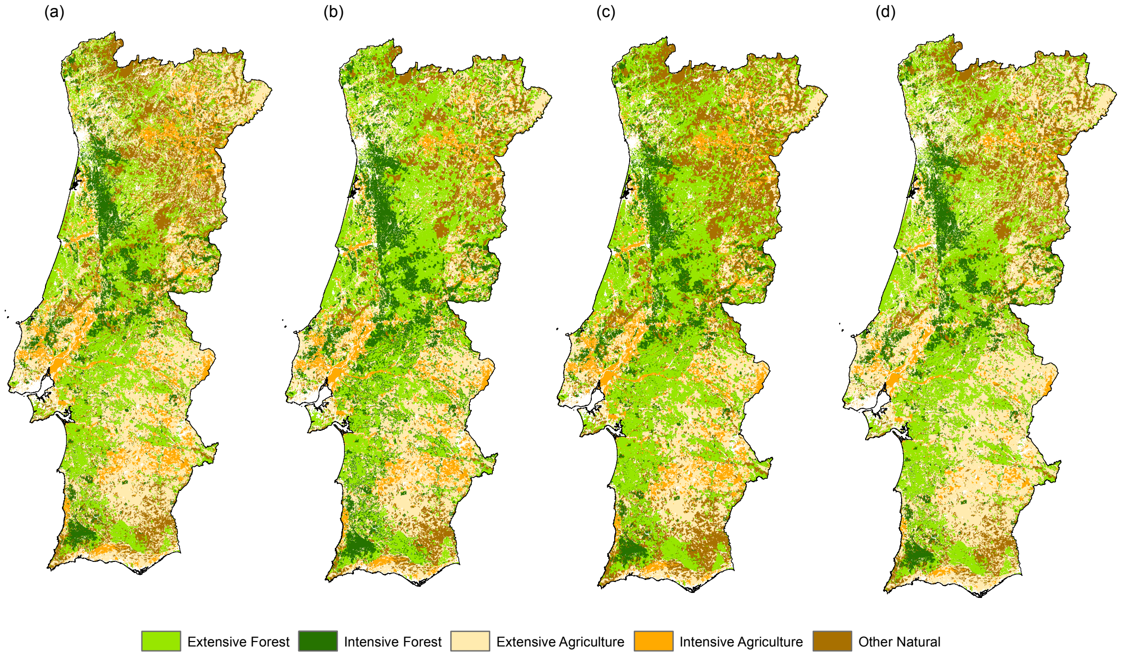

Fig. 1. Land-uses in Portugal in the baseline (**a**; 2010), in the Pathway 0 by 2050 (**b**), in the Pathway A in 2050 (**c**) and in the Pathway B in 2050 (**d**)

In Pathway B, and following the behavioral changes associated with the underlying scenario, the overall area of agriculture remains relatively stable compared to 2010 (43.4% in 2050 *vs* 44.3% in 2010, Table 1 and Table SM3). However, the high rate of extensification of agriculture areas projected to occur (i.e., loss of 50% of all intensive agriculture areas) as expected by the 'land sharing’ approach of pathway B, lead to an increase in the country’s multifunctional areas, particularly in the central and southeast part of Portugal. From 34.5% in 2010, it increases to 38.4% in 2050, which represents an overall increase of 11.5% in extensive agriculture areas during the time period considered.

Biodiversity change

In all scenarios, on average across 10 km x 10 km cells, the total alpha species richness is projected to increase, with species responses to land use change varying in intensity and even in direction across different regions of Portugal (Figs. 2 and 3, Table S3).

In Pathway 0, on average, forest species richness is projected to increase, while both farmland species richness and the richness of other species are projected to decrease (Fig. 2, Table S3). In the north-northeast and southeast of Portugal, alpha species richness increases, with increases in both forest and other bird species, due to agricultural land abandonment leading to an increase of both natural and extensive forest areas. However, as more area is converted to forest (intensive and extensive) species richness of other birds decreases, particularly across the northwest, center and southwest of Portugal, thus leading to a reduction, on average, in the national levels of other species richness (Fig. 3). Farmland species loss seems to be more equally distributed across the country, as agriculture areas decrease in all regions of Portugal.

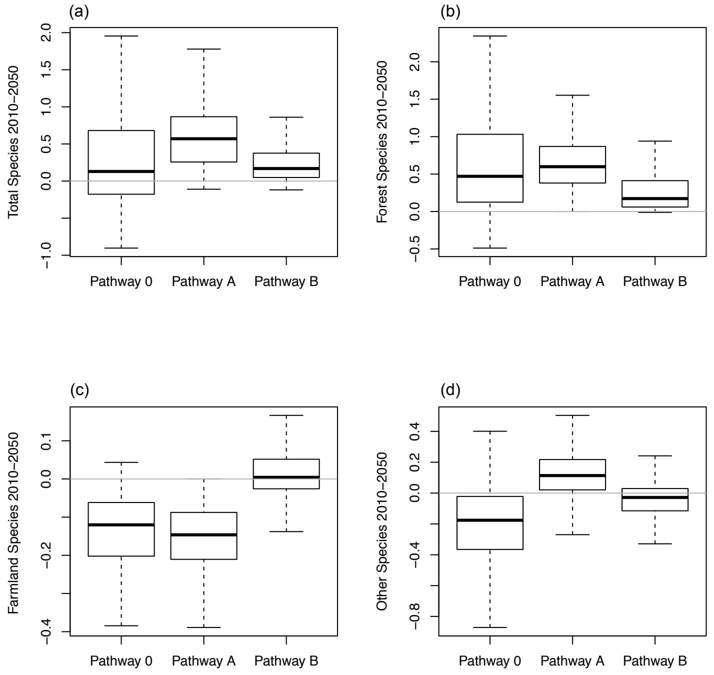

Fig. 2. Change in alpha species richness of the different species groups between the baseline 2010 and the different pathways: Total species (**a**), forest species (**b**), farmland species (**c**) and other species (**d**). Unit: number of bird species.

While, Pathway 0 and Pathway B result in similar average increases in alpha (+0.82% s.d.=1.72, and +0.69% s.d.=0.70, respectively) and gamma (+0.34% and +0.40%, respectively) bird species richness, they show two distinct spatial patterns (Figs. 2 and 3, Table S3).The changes in alpha species richness in Pathway B are more moderate across the entire country (Fig. 3), with farmland species richness projected to increase, and both forest species richness and the richness of other species projected to decrease (Table S3). In pathway B, the gain of forest species is centered in the north-northeast part of the country, were extensive forest is still projected to increase as result of natural succession, with only small changes occurring in the rest of the country. The state of farmland species is projected to improve, as multifunctionality, particularly in the central and southeast part of Portugal, increase both the area and niches available to these species. Still, small losses of farmland species occur in this scenario, but they mostly happen in the north-northwest part of Portugal, where some agricultural land abandonment is still projected to occur (Figs. 1 and 3).

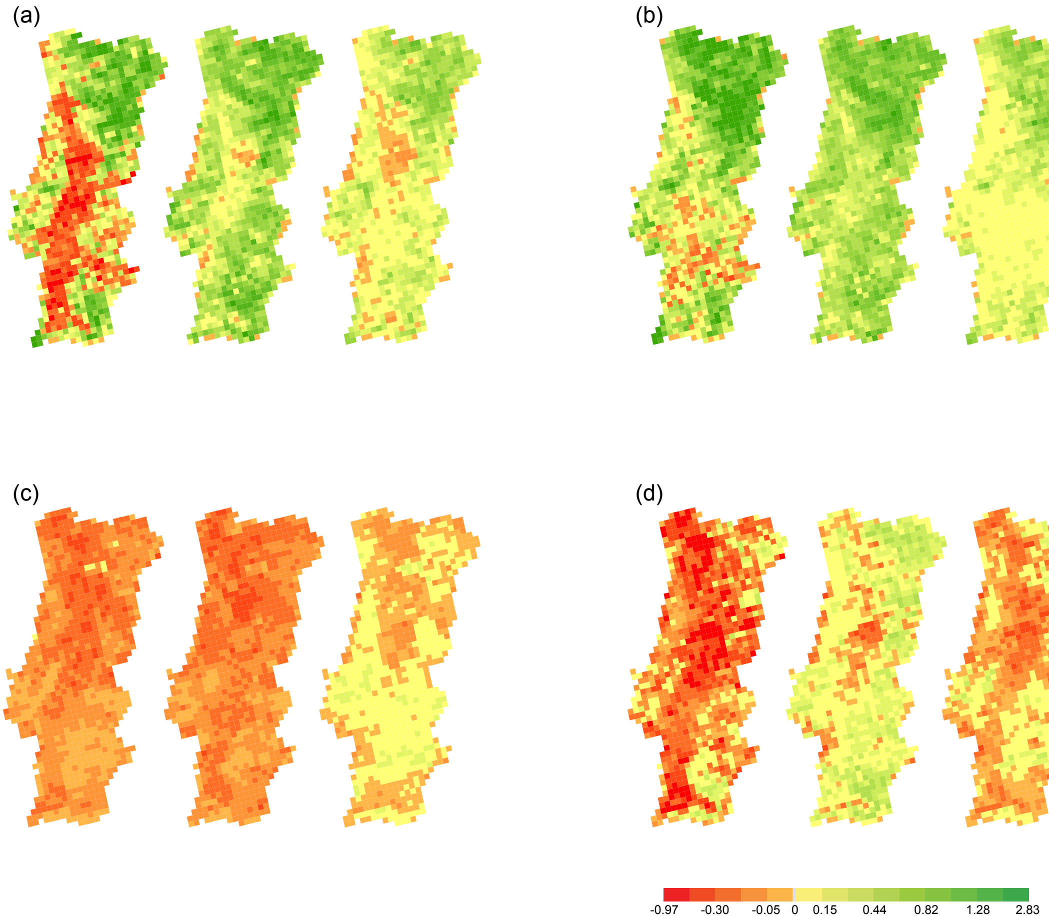

Fig. 3. Map of the difference between the species richness relative to the 2010 baseline for Pathways 0, A, and B in each 10 km x 10 km grid-cell: Total species (**a**), forest species (**b**), farmland species (**c**) and other species (**d**). From left to right: Pathway 0, Pathway A, and Pathway B. Unit: number of bird species.

Finally, the technological improvement scenario (i.e., Pathway A) results in the highest values of biodiversity change (i.e., +1.70% s.d.=1.15 at the local scale and +1.57% at the national scale; Table S3). In this scenario, both the forest species richness and the richness of other species are projected to increase, while farmland species richness is projected to decrease, but not as much as for Pathway 0 (Table S3, Fig. 3). Here, changes in both forest species and farmland species occur in all regions of Portugal, as the loss of agricultural areas leads to an increase in both natural areas and extensive forest areas. Consequently, other species richness increase, particularly in the northeast and southeast of Portugal, as natural areas increase.

Discussion

Many pathways have been proposed for navigating the way to a sustainable food system (Fraser *et al.* 2016). Some scholars advocate for more radical changes such as new technological systems, genetic engineering or precision farming (Fedoroff *et al.* 2010), whereas others argue that agricultural production does not need a revolution and that we simply need to improve current farming practices (Connor and Mínguez 2012). Others, still, argue for organic agriculture (Hole *et al.* 2005) or local food systems (Halweil 2002). Here, we highlight that whichever pathway is chosen to achieve a sustainable future it will have important and differential impacts on biodiversity.

In our analysis, although species richness was projected to increase in all scenarios, we show that different pathways will favor different species groups. For instance, in the technical component substitution scenario (Pathway A), species associated with "natural areas" (e.g., forest species and other species) were projected to expand as more habitat becomes available, as a result of the increase in farmland abandonment and consequently natural habitats. On the contrary, farmland species that rely on open habitats would likely see their range restricted to the more intensively used agricultural areas, and the species more sensitive to change would likely disappear, thus not differing from a business-as-usual scenario.

The broader regime transformation scenario (Pathway B) suggests that a multifunctional landscape would be able to sustain species richness by supporting more habitat heterogeneity and thus increasing the niches available to the different species groups. However, we show that this scenario would clearly favor farmland species over other species groups. In Pathway B, the state of farmland species is projected to improve, a trend not present in the two other scenarios. Nonetheless, the projected increase in the richness of forest species observed with the other scenarios will be lessen in Pathway B, as less area is released from human pressure and made available for natural succession and forest expansion. In short, changing to a more intensive farming system would cause a loss of farmland species and a gain in forest and other species. In contrast, a strategy aimed at extensive agriculture and integrating farming with biodiversity functions would favor farmland species, while forest species might decline. Note that while most species may persist in the landscape even after significant land use changes, large variations may occur in the relative abundance of species, a variable that is not tracked by our model.

Species diversity is key for a rich and diverse set of ecosystem services (Mace *et al.* 2012), therefore it is essential to aim for a diversity of habitats in order to sustain higher levels of biodiversity, while ensuring the benefits for people that ecosystems provide. A single land use strategy, whether land sparing or sharing, cannot ensure the conservation of all species (Salles *et al*. 2017). It is unavoidable that there will be some loser species independently of the chosen plan of action, therefore, conservation efforts should be implemented to safeguard these species and/or strategies to maintain their habitats requirements within the landscape, thus minimizing losses. For instance, the impact on farmland species could be mitigated by maintaining patches of extensive agriculture, or by reintroducing large herbivores to limit secondary succession (Navarro *et al.* 2015; Svenning *et al.* 2016). Additionally, the impact on forest and other non-farmland species could be lessened by expanding the current protected areas network in order to maintain natural areas.

Although there are different management strategies for preventing further loss of biodiversity, it is also clearly not preferable or even possible to implement the same measures everywhere. The national and sub-national landscape context needs to be taken into account in the development of policies promoting a given conservation measure. In line with much of the recent discussion around the "land sparing *versus* land sharing" framework (e.g., Fischer *et al.* 2014; Kremen 2015), we argue that both approaches should not necessarily be mutually exclusive at larger scales since their potential impacts on biodiversity are context dependent. In Portugal, land sparing strategies present interesting opportunities, as there is enough margin for intensification on existing agriculture areas while the abandonment of marginal and less productive lands would present an opportunity for rewilding and conservation (Merckx and Pereira 2015). However, such strategy is likely to mainly benefit biodiversity in the center and north of Portugal, regions currently under large-scale farmland abandonment pressure (Pereira *et al.* 2009). In contrast, most of the south of Portugal is characterized by *Montados*, a well-established agro-forestry system (i.e., land sharing strategy). This multifunctional landscape not only supports high levels of biodiversity and ecosystem services, but plays an important role in the Portuguese economy (Pinto-Correia *et al.* 2011).

Projecting the future of the landscapes under a range of scenarios is a key step towards making management decisions that are likely to promote biodiversity and ecosystem services (van Vuuren *et al.* 2012; Rosa *et al.* 2017), and a useful tool for policy- and decision-makers to predict the impact of their actions prior to their implementation. On the basis of this analysis, we argue that any attempts at improving national biodiversity levels (or species richness) through conservation or management actions, should take into account regional differences not only in terms of species and ecosystems present, but also socio-economic dynamics that might be impacted by such actions. To improve conservation guidance, coordinated regional planning and cooperation across sectors of the economy (e.g., forestry and agriculture) is essential, particularly to anticipate where to target and which species would be more impacted by possible management decisions.

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Chapter 6

Synthesis

This dissertation presents methods to improve the quantification of local, regional and global biodiversity loss due to land use change as well as improves our knowledge of how not only total species, but also different species groups, respond to land use change. In particular, the application of the countryside SAR is demonstrated in various case studies, which serve not only as a vehicle to illustrate the methods, but also provide findings relevant for assessing global environmental challenges.

6.1 Biodiversity in human-modified landscapes

Land use change is an undisputed major driver of biodiversity change, affecting species richness patterns from local to global scales (Pereira *et al.* 2012). Globally, biodiversity has been declining steadily (Pimm *et al.* 2014) yet recent case studies at local scale have reported mixed patterns and trajectories of net change in species richness, with some studies reporting no changes in local diversity loss while other report declines (e.g., Dornelas *et al.* 2014; Newbold *et al.* 2015). Recent works have suggested that much of the current disagreement is due to the variety of land use options being explored in various regions and the various temporal and spatial scales being analyzed (Gonzalez *et al.* 2016; Cardinale *et al.* 2018). Here, the different habitat preferences of species and the capacity of the modified habitat to support them are shown to be crucial considerations as well (Chaps. 2, 3 and 5). For instance, positive responses of species to human-modified habitats are commonly attributed to an increase in the carrying capacity of the habitat (e.g., structurally complex habitats provide more niches to species), where new species can live or coexist with the existing native species (Tews *et al.* 2004; Stein *et al.* 2014). However, in most cases, species with narrower niches are more likely to go locally extinct after habitat change (Devictor *et al.* 2008), changing local species composition (e.g., when forest is converted to cropland, farmland bird species may increase their richness while forest bird species decrease theirs; Chap. 5). Thus, even if the average local species richness is not always, or even often, declining in concert with global gamma declines, species loss is not random with regard to identity and functional performance (Hillebrand *et al.* 2018). Such insights are of particular importance, as changing species composition may have major consequences for ecosystem functioning (e.g., reduction in genetic diversity or homogenization of species composition at local scales) (Hooper *et al.* 2012; Cardinale *et al.* 2012; Tilman *et al.* 2014). Conservation efforts should be implemented to safeguard these species and/or strategies to maintain their habitats requirements within the landscape, thus minimizing losses.

Moreover, land use change impacts may depend on other aspects such as the environmental, historical and socioeconomic context (Chap. 5; Stein *et al.* 2014; McClanahan and Rankin 2016; Ramankutty *et al.* 2018). Therefore, any attempts at improving biodiversity levels, through conservation or management actions, should take into account regional differences not only in terms of species and ecosystems present, but also socioeconomic dynamics that might be impacted by such actions (Chap. 4 and 5).

6.2 Scaling biodiversity responses to habitat conversion

Land use activities can result in local, regional, or global species richness change. Global or regional extinction rates are often modeled using Species-Area relationship (SAR) models (Millennium Ecosystem Assessment 2005; van Vuuren *et al.* 2006). If the proportion of species going extinct was constant with scale, the SAR model would project a monotonic increase of the number of species going extinct with scale. However, empirical studies have suggested that as the spatial grain increases, the effect of land use on biodiversity patterns can follow both a non-monotonic and non-linear relationship with sampling grain (i.e., spatial sampling window) (Chaps. 2 and 3; Keil *et al.* 2018). Hence, how species perceive the landscape and are impacted by habitat conversion is a scale-dependent phenomenon (i.e., changes across sampling scales or grain of analysis). Such results imply that a simple interpolation of extinction rates between grains or an extrapolation of extinction rates at grains for which we have limited data should be done with caution, if at all.

This non-linearity of proportion of species extinction with sampling scale calls for some caution when plotting the reduction in species richness using grid cells (e.g., 50 km × 50 km or larger) based on plot level responses to land-use change (e.g. Alkemade *et al.* 2009; Newbold *et al.* 2015), as the reductions at those scales may be significantly smaller than those at the plot scale (Chap. 3). As, plot level biodiversity loss might just be due to displacement (e.g., forest specialist species relocating to nearby remaining natural forest if a part of its original distribution range is now used for agriculture), and therefore not detected at larger scales.

Moreover, and on the basis of the analyses performed in this dissertation, it is clear that when modeling biodiversity responses to habitat conversion, one has to consider that the impacts of land use change on biodiversity at a larger scale and within the context of heterogeneous landscapes may be different than plot-scale effects (Chap. 3; Thomas, 2013). These results are particularly relevant for the current debate over local biodiversity change (Cardinale et al. 2018), where recent analyses of time series datasets have not found evidence of systematic declines in local species richness (Vellend et al. 2013; Dornelas et al. 2014; Elahi et al. 2015; Hillebrand et al. 2018). The large variance across space and time (e.g., Dornelas et al., 2014) as well as across land use types (e.g. Chap. 3; Newbold et al., 2015) in plot based species richness studies calls for caution when interpreting species richness trends from local studies (Chase and Knight 2013; Gonzalez *et al.* 2016; Hill *et al.* 2016). When using simplistic measures, such as species richness (Hillebrand *et al.* 2018), it Is also essential to keep track of the contributions of different species (e.g. specialist *versus* generalists species) to biodiversity trends, as these trends can tell very distinct stories with different implications for conservation (Chap. 5; Section 6.1).

In this dissertation, the countryside SAR model, as a modification of the classic SAR model, was presented and tested as a unifying framework to account both for the effects of species persistence on the matrix and for the non-linear relationship between habitat area and species richness (see section 6.3).

6.3 Assessing biodiversity responses to habitat change using the countryside SAR approach

SAR models are an important tool for predicting biodiversity change after habitat conversion. Yet, the assumption that the modified landscape is completely inhospitable is undoubtedly overly simplistic (Pereira and Borda-de-Água 2013). In most real-world situations, land use change results in a mosaic of several habitat types with variable degrees of suitability for different species (Pereira and Daily 2006; Koh and Ghazoul 2010). Here, it is shown that integrating varying land use effects into a SAR-model leads to considerable improvement of the prediction of species richness patterns at larger scales (Chap. 2), findings that align with previous local scale research (Guilherme and Pereira 2013; Proença and Pereira 2013). In addition, by considering the differential use of habitat by different species groups, the countryside SAR model allows a more precise detection of community responses to land use change (Chap. 5) and hence gives a much more holistic picture than the classic SAR-model.

Using the model framework developed in this dissertation, more detailed and multi-scale assessments of the impacts of socioeconomic developments on biodiversity can be achieved (Chaps. 4 and 5). The countryside SAR model can be used to project biodiversity changes, not only from the loss of native habitat but also from an increase in modified habitats, such as farmland areas (Chaps. 4 and 5), as long as those habitats are incorporated into the model and the affinities of the species for those habitats are calculable. Moreover, the countryside SAR model can help identify particular land use types that are driving biodiversity loss between different regions of the world (Chaps. 4 and 5). For example, data like the characterization factors[1] calculated in Chapter 4 can be used by conservation organizations as well as policy- and decision-makers to quantify, compare and potentially reduce the biodiversity footprint of certain socioeconomic activities. The countryside SAR model can also be used to identify which species functional groups are likely to be the winners or losers of particular socioeconomic developments, thus directing conservation efforts towards the relevant species and ecosystems impacted. This is important because the rates of change in species composition are often decoupled from changes in richness (Hillebrand *et al.* 2018).

Biodiversity change projections from the countryside SAR may be less catastrophic than classic SAR but they are certainly more realistic (Chaps. 2 and 5; Guilherme and Pereira 2013; Proença and Pereira 2013; Pereira *et al.* 2014) and will ultimately allow for better-informed decision-making (Chaps. 4 and 5).

6.4. Projecting biodiversity change in a teleconnected world

Projecting the future of the landscapes under a range of scenarios is a key step towards making management decisions that are likely to promote biodiversity and ecosystem services (van Vuuren *et al.* 2012; Rosa *et al.* 2017). Thus, it is fundamental that policy- and decision makers have the tools and knowledge available to assess how certain decision or specific plans of action can affect the future of biodiversity. Not only, if ‘business as usual’ trends persist (i.e., population growth, economic growth, land use change trends), but also if specific certain more “radical” actions are put in place (i.e., change in consumption patterns, or farming practices).

On the other hand, the environmental and socioeconomic interactions between world regions (i.e., telecoupling) are increasing dramatically. Such teleconnections, through international trade, lead to an increasing disconnect between production and consumption, resulting in complex causal interrelationships that can hampering straightforward analyses (Chap.4, Moran and Kanemoto

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[1] Characterization factors (CFs): Number of birds potentially extinct per km^2 of area used by land use activity.

2017). Such teleconnections between regions are interlinked with current patterns of land use (e.g., palm oil demand in Europe and its consequences for producing countries; Chap. 4). Therefore, understanding the biodiversity impacts inflicted by consumption in individual countries and embodied in international trade is essential to not only inform future conservation guidance, but also to project biodiversity responses to changes in production methods or consumption patterns (Chap. 4; Bateman *et al.* 2015; Chaplin-Kramer *et al.* 2015). For example, Chapter 4 results show that targeting cattle farming for minimization of impacts would have the highest positive impact, as it contributes to 28% of total biodiversity impacts, mostly in Central and South America and in Africa.

While, in an increasingly globalized world, global assessments of biodiversity and ecosystem services are relevant for coordinated policies and sharing responsibility (Chap. 4). The impact of agricultural and forestry activities on local species communities can differ depending upon the regional socioeconomic context (Chaps. 4 and 5). Further, regional and local assessments can help guide *in-situ* conservation efforts and determine the extent to which species at finer scales should be targeted. The approach presented in Chapter 5 allows the study of how alternative future scenarios of land use change might affect biodiversity, as well as the trade-offs with biodiversity resulting from national and international policy changes, across a vast geographic area. However, it only assesses the impacts from changing production activities taking place within a region. Forthcoming studies can contribute to its improvement by integrating the different regional production-consumption interlinkages identified in Chapter 4 in future scenarios of land use change. As consumption patterns changes in a country will undoubtedly influence the production patterns in other countries, such analyses have the potential to unravel the impacts on species richness and community composition of future changes in global trade.

Furthermore, while it is unavoidable that future socioeconomic developments will lead to further biodiversity change, different choices can impact species differently. Therefore, assessing the impact of such developments on different species communities (e.g., specialist *versus* generalists species) by using the countryside SAR framework presented in this dissertation, will help anticipate changes and guide conservation in order to safeguard the “loser” species.

6.5 Policy relevance of the research

Continued global biodiversity loss has led to several international agreements aimed at halting this trend (CBD 2010; UN General Assembly 2015). The results and methods of the dissertation are particularly relevant to achieving several of the Aichi Biodiversity Targets for 2020. For instance, the dissertation presents several insights into global land use and its impacts on local, regional or global species richness. Such findings can be used to create awareness regarding the values of biodiversity and conservation by making explicit which land use activities and products contribute most to biodiversity change (*Aichi Target 1*). The biodiversity-socioeconomic trade-offs explored in Chapter 4 and 5 are particularly relevant to policy- and decision makers. For instance, the insights gained from Chapter 4 can be used by governments to consider remote responsibility in an equitable way, when implementing plans for sustainable production and consumption (*Aichi Target 4*). Similarly, the teleconnections identified between world regions can be used, for example, as a guide by production countries to devise mitigation strategies or by consumption countries to fund conservation actions or help offset biodiversity impacts. On the consumption side, this work can help raising consumer awareness regarding the hidden impacts in imported products they buy (*Aichi Target 1*).

Furthermore, the case-study of Portugal in Chapter 5 highlights how biodiversity impacts may differ depending upon the intervention plan and the regional social-economic context. Analyses such as the one performed in this dissertation can be used to inform national and local development plans to promote the sustainable use of resources while at the same time intending to minimize or halt biodiversity loss (*Aichi Target 2*). Overall the methods and findings of this dissertation help advancing the understanding of the impacts of different land use types and activities on nature, including the status and trends of biodiversity (*Aichi Target 19*), while providing decision support tools for the sustainable management of agriculture and forestry (*Aichi Target 7*). Finally, such methods and tools have the potential to improve global analyses of biodiversity change, which are especially needed to inform future conservation goals (e.g., post- 2020 Aichi Targets) and ongoing policy-driven assessments (e.g., IPBES Global Assessment and the work by the IPBES Expert Group on Scenarios and Models; Kim *et al*. 2018; Martins *et al*. 2018; Pereira *et al*. 2018).

6.6 Critical Appraisal

Biological diversity is a multifaceted concept, which includes *"the variability among living organisms from all sources including, inter alia, terrestrial, marine and other aquatic ecosystems and the ecological complexes of which they are part; this includes diversity within species, between species and of ecosystems"* (CBD 1992). Because the multidimensionality of biodiversity poses formidable challenges to its measurement, a variety of surrogate or proxy metrics are often used. These include the species richness of specific taxa. However, one of the limitations of using just changes in species richness as an indicator is that it provides information about only a small aspect of biodiversity, thus not capturing key attributes such as changes in abundance, composition, and community structure that may lead to further biodiversity impacts. The approach adopted in this dissertation partially overcomes these limitations by assessing species richness change within and between functional species groups. By considering the differential use of habitat by different species groups, the countryside SAR model allows a more mechanistic linking between ecosystem processes and species loss and thus a more precise detection of community response to land use change. However, the limitation here is that currently this method is only applicable when data on individual species habitat preferences is available (e.g., habitat preferences information provided by BirdLife or listed in Atlas as used in chapter 2), which is often challenging to obtain, and when habitat affinities of different species groups for natural and human-modified habitats are known or calculable.

By using bird species as a single functional group, the analysis in Chapter 4 assumes that all bird species share a single response towards land use change. Although crude, the consideration of a single functional group was necessary due to a lack of readily available global data for our approach. The countryside SAR originally separates species into functional groups with different affinities for natural and human-modified habitats (Pereira and Daily 2006). Such affinities can be retrieved by model fitting (Chap. 2), or can be estimated from plot-scale pairwise comparisons of local species richness in native and human-modified habitat (Chap. 3). The former relies on field or atlas data of species frequencies in different habitats to quantify habitat affinities (yet such data is scarce at continental scales), while the latter relies on knowing the identity of the species present in the local plots. However, databases of such plot-scale studies often group species by taxon, neglecting to report species identity, and therefore making it impossible to group species accordingly with their habitat preferences. Recent efforts, such as the PREDICTS database (Hudson *et al.* 2014), which aims to compile responses of local terrestrial biodiversity to human induced disturbances, are crucial. Only with these databases with detailed knowledge of site-specific species composition data, can species be grouped according to their habitat preferences before affinities estimates are calculated. These improved estimates of species affinities will significantly reduce the uncertainty in future assessments of biodiversity change.

Moreover, birds were used as an indicator taxa in this dissertation. This decision was in part due to limited data availability for other taxonomic groups, but also because birds have clear associations to specific land uses and because birds are useful indictors for broader biodiversity (Pereira and David Cooper 2006; BirdLife International 2013). Although current information does not permit more detailed global analyses, the methods presented here provide the means to undertake such analyses as the information becomes available.

6.7 Final remarks

The complexity of studying biodiversity change across scales and habitats should not be underestimated. It is empirically challenging and requires a solid theoretical background. This dissertation contributes to a deeper understanding of species-area relationship models and their applicability when assessing and/or projecting species responses to habitat change as a result of socioeconomic activities. The countryside SAR framework presented here emerges as a unifying framework that retains the heuristic property of the classic SAR model, while being capable of accounting for the wider effects of the landscape on biodiversity. Conservation policies and prioritization strategies that focus on overall species richness alone might lead to incomplete or misguided understanding of biodiversity change. A research priority is, of course, understanding the contributions that different species (e.g., specialists and generalists) make to observed biodiversity trends, as these can have different implications for conservation (Hillebrand *et al.* 2018; Cardinale *et al.* 2018). This dissertation addresses this priority and uncovers important insights from which conservation can benefit. Above all, conservation and prioritization strategies that consider a broad spectrum of habitat responses from multiple species groups have the potential to be more successful in safeguarding the multiple levels of biodiversity. Finally, the considerations presented in this work are highly relevant for monitoring the status and trends of biodiversity and improving conservation guidance, in particular by allowing for more meaningful assessments of biodiversity change.

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I will like to give a special thanks to a few people. Vânia, for all her support and guidance during my first steps, and for showing me what research actually was. Luis, who showed me that programing could be fun and for the never-ending willingness to help. A special thanks also to Laetitia, from late night concerts of Queen to bone chilling monopoly games, your exuberance, support and friendship have truly made a difference in my life. Alexandra (Aleki), for all the support, good advice and for making me laugh when I needed the most. Thank you for sticking up with me throughout this journey (and for sharing Miuki with me). Special thanks to Murilo and Silvia, with whom I had the honor of sharing this journey. We not only move to Leipzig together, but as fellow PhD students we shared fears, experiences, and all the ups and downs of being an early stage researcher. Florian and Andrea, for constantly pushing me to go out and enjoy live outside work as well as for the great company overall. I can now concede that several German stereotypes are plain wrong. Also, Florian, I'm still waiting for my "How are you?" routine. I would like to thank Angela, for the silly conversations and coffees and the happy friendship that was born from there. I will be forever grateful to Red, and I’m still annoyed for the 2 months we wasted. Shopus also deserves a special mention, particularly after his willingness to spell check my work and the overwhelming positivity and kindness in these last months. Finally, I will like to give a very special thanks to Isabel, who become an amazing source of inspiration as well as support, both personally and professionally. In the last 2 years, your company and friendship have truly made my life much richer (and fun). A special thanks also to the “Upside down” group for being a ray of sunshine when I needed it, and to the “Masterminds” group for the safe space it provides, the overwhelming support, the advices and the disposition to revised my drafts exhaustively.

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Last but not least, I will to thank my family for all their love and unconditional support. In particular, my parents, Lina and Mário, my brother bear, Artur, and my sister, Tânia. Despite all my jokes, I truly feel you are the better person. Finally, I would like to give a very warm thank you to my grandmother Maria, who not only though me the value of nature, but whose love and teachings mold me in the person I am today.

Appendix

A. Supplementary material for chapter 2

Supplementary data

Table 1: The land use classification used in the study. Original land use classes were aggregated in four main land cover categories: Agriculture land, uncultivated land, forest and exotic forest.

Aggregated land use category	**Original land use category for Portugal**	**Original land use category for Spain**
Agriculture land (AG)	Arable land, annual crops, permanent crops, heterogeneous agricultural areas, olive grove, vineyard, orchard, other shrubs, permanent grassland, agro-forestry areas (where agriculture area dominate).	Agriculture land.
Uncultivated land (UL)	Poor rangeland, low shrub, sclerophyllous vegetation, high shrub and degraded or transition forest, uncovered areas with little or no vegetation, abandoned olive grove, recently burned areas.	Land with scrub species and / or natural grassland or weak human intervention, pasture or grass mixed with brush, scrub and/or herbaceous vegetation associations, open spaces with little or no vegetation.
Forest (F)	*Quercus ilex, Quercus suber, Quercus sp. , Castanea sativa, Pinus pinea, Pinus pinaster,* other brodleaf and coniferous species.	Coniferous and broadleaf mosaic, Eucalypt/pine, mixed coniferous, other pine and coniferous, species, *Pinus nigra* and *Juniperus thurifera*, mix of other pine species, pine repopulation, other pine, *P.halepensis* and *P.nigra*, *P.halepensis* and *P.sylvestris*, *P.nigra* and *P.sylvestris*, *P.pinea* and *P.halepensis*, *P.pinea* and *P.nigra*, *P.pinea* and *P.pinaster*, *P.pinea* and *P.sylvestris*, *P.pinaster* and *P.halepensis*, *P.pinea* and *P.nigra*, *P.pinea* and *P.sylvestris*, *P.sylvestris* and *P.uncinata*, *Pinus halepensis, Pinus radiate, Pinus nigra*, *Populus nigra, Pinus pinea, Pinus pinaster, Pinus sylvestris, Pinus uncinata, Abies alba, Juniperus thurifera*, Riparian forest, Mixed broadleaf species, Broadleaf and riparian forest mosaic, *Q.robur* with *Q. Petraea* and *Betula spp*, *Q.canariensis* and *Olea europea*, Oak forest and *C.sativa*, *Quercus suber* and other broadleaf, Oak forest and *F.sylvatica*, *Q.ilex*, *Q.pyrenaica*, *Q.faginea* and *Q.suber*, *Q.robur* and *Q.petraea*, *Q.suber* and *Q.faginea*, *Q.pyrenaica* and *Q.faginea*, *Q.ilex* and *Q.faginea*, *Q.ilex* and *Q.petraea*, *Q. ilex* and *Q.suber*, *Quercus ilex*, *Quercus suber*, *Quercus pyrenaica*, *Quercus faginea*, *Castanea sativa*, *Fagus sylvatica*, *Olea europaea.*
Exotic forest (EF)	*Eucalyptus sp.*	Mixed Eucalyptus species, *Eucalyptus globulus*, *Eucalyptus camaldulensis.*

Table 2: Models used to test the role of environmental variables in species richness. Predictors were grouped into 3 environmental categories to reflect ecological meaning.

Competing models		Predictors	Type of Aggregation
M_C	Climatic Predictors	***Tmp.medjl*** (mean temperature in July) ***Tmp.ran*** (annual temperature range) ***Pre.ann*** (annual precipitation)	Weighted mean of subpixels (ºC) Weighted mean of subpixels (ºC) Weighted mean of subpixels (mm)
M_T	Topographic Predictors	***Alt.mea*** (mean elevation) ***Rad.mea*** (mean radiation index) ***Rad.ran*** (range of the radiation index)	Mean of subpixels (m) Mean of subpixels Mean of subpixels
M_H	Habitat Predictors	***Agr.sum*** (proportion of Agricultural land) ***Unc.sum*** (proportion of Uncultivated land) ***For.sum*** (proportion of Forest) ***Exo.sum*** (proportion of Exotic forest)	sum of subpixels (%) sum of subpixels (%) sum of subpixels (%) sum of subpixels (%)
M_{CT}	Climatic Predictors Topographic Predictors	***Tmp.medjl; Tmp.ran; Pre.ann*** ***Alt.mea; Rad.mea; Rad.ran***	
M_{CH}	Climatic Predictors Habitat Predictors	***Tmp.medjl; Tmp.ran; Pre.ann*** ***Agr.sum; Unc.sum; For.sum; Exo.sum***	
M_{TH}	Topographic Predictors Habitat Predictors	***Alt.mea; Rad.mea; Rad.ran*** ***Agr.sum; Unc.sum; For.sum; Exo.sum***	
M_{CTH}	Climatic Predictors Topographic Predictors Habitat Predictors	***Tmp.medjl; Tmp.ran; Pre.ann*** ***Alt.mea; Rad.mea; Rad.ran*** ***Agr.sum; Unc.sum; For.sum; Exo.sum***	

Table 3: Multiple R^2 values from all OLS models when including second-order polynomials (quadratic terms), for each taxonomic group at the grain size of 10 km x 10 km; △AIC values and the lowest AIC (in parentheses) for each taxa are also shown. Model designation refers to the different sets of predictors (climate (M_C), topographic (M_T) or habitat (M_H)), considered individually and jointly, used to account variation patterns (in all cases $P < 0.001$).

	Clim. (**M_C**)		Topo. (**M_T**)		Habit. (**M_H**)		Clim. & Topo. (**M_{CT}**)		Clim. & Habit. (**M_{CH}**)		Topo. & Habit. (**M_{TH}**)		Clim. & Topo. & Habit. (**M_{CTH}**)	
	R^2	△AIC	R^2	△AIC	R^2	△AIC	R^2	△AIC	R^2	△AIC	R^2	△AIC	R^2	AIC
Amphibians	0.20	420	0.08	1188	0.18	565	0.22	282	0.24	81	0.20	403	0.25	$0^{(29302)}$
Reptiles	0.12	1077	0.20	545	0.08	1345	0.24	221	0.21	443	0.24	260	0.27	$0^{(33153)}$
Passerines	0.39	685	0.32	1350	0.20	2317	0.44	250	0.44	254	0.37	877	0.46	$0^{(39674)}$

Table 4: List of the 87 passerine species considered in the analysis. Abbreviations: Classification by affinity group (AL- agriculture land; UL-uncultivated land; F-forest) and country were they occur (PT-Portugal; SP-Spain). Species were assigned to their group according with the literature and expert opinion.

Species	Species code	Region	Affinity group
Aegithalos caudatus	AEGCAU	PT/SP	F
Alauda arvensis	ALAARV	PT/SP	UL
Anthus campestris	ANTCAM	PT/SP	AL
Anthus spinoletta	ANTSPI	PT/SP	AL
Anthus trivialis	ANTTRI	PT/SP	F
Calandrella brachydactyla	CALBRA	PT/SP	UL
Callipepla californica	CALCAL	SP	UL
Carduelis cannabina	CARCAN	PT/SP	UL
Carduelis carduelis	CARCAR	PT/SP	AL
Carduelis chloris	CARCHL	PT/SP	AL
Certhia familiaris	CERFAM	PT/SP	F
Cercotrichas galactotes	CERGAL	SP	F
Cettia cetti	CETCET	PT/SP	UL
Chersophilus duponti	CHEDUP	SP	UL
Cisticola juncidis	CISJUN	PT/SP	UL
Corvus frugilegus	CORFRU	SP	F
Corvus corax	CORCOR	PT/SP	UL
Corvus monedula	CORMON	PT/SP	AL
Cyanoliseus patagonus	CYAPAT	SP	F
Emberiza calandra	EMBCAL	PT/SP	AL
Emberiza cia	EMBCIA	PT/SP	UL
Emberiza cirlus	EMBCIR	PT/SP	AL
Emberiza citrinella	EMBCIT	PT/SP	UL
Emberiza hortulana	EMBHOR	PT/SP	UL
Erithacus rubecula	ERIRUB	PT/SP	F
Ficedula hypoleuca	FICHYP	SP	F
Fringilla coelebs	FRICOE	PT/SP	F
Galerida cristata	GALCRI	PT/SP	AL
Galerida theklae	GALTHE	PT/SP	UL
Garrulus glandarius	GARGLA	PT/SP	F
Hippolais pallida	HIPPAL	PT/SP	UL
Hippolais polyglotta	HIPPOL	PT/SP	UL
Lanius collurio	LANCOL	PT/SP	AL
Lanius excubitor	LANEXC	PT/SP	AL
Lanius senator	LANSEN	PT/SP	AL
Locustella naevia	LOCNAE	SP	AL
Loxia curvirostra	LOXCUR	PT/SP	F
Lullula arborea	LULARB	PT/SP	AL
Luscinia megarhynchos	LUSMEG	PT/SP	F
Luscinia svecica	LUSSVE	PT/SP	UL
Melanocorypha calandra	MELCAL	PT/SP	UL
Montifringilla nivalis	MONNIV	SP	UL
Monticola saxatilis	MONSAX	PT/SP	UL
Motacilla alba	MOTALB	PT/SP	AL
Motacilla cinerea	MOTCIN	PT/SP	UL
Motacilla flava	MOTFLA	PT/SP	AL
Muscicapa striata	MUSSTR	PT/SP	F
Oenanthe hispanica	OENHIS	PT/SP	AL
Oenanthe leucura	OENLEU	PT/SP	UL
Oenanthe oenanthe	OENOEN	PT/SP	UL
Oriolus oriolus	ORIORI	PT/SP	F
Parus ater	PARATE	PT/SP	F
Parus caeruleus	PARCAE	PT/SP	F
Parus cristatus	PARCRI	PT/SP	F
Parus major	PARMAJ	PT/SP	F
Parus palustris	PARPAL	SP	F
Passer montanus	PASMON	PT/SP	AL
Petronia petronia	PETPET	PT/SP	UL
Phoenicopterus roseus	PHOROS	SP	F
Phylloscopus bonelli	PHYBON	PT/SP	F
Phylloscopus collybita	PHYCOL	PT/SP	F
Phylloscopus ibericus	PHYIBE	PT/SP	F
Pica pica	PICPIC	PT/SP	F
Prunella collaris	PRUCOL	SP	UL
Prunella modularis	PRUMOD	PT/SP	UL
Pyrrhocorax graculus	PYRGRA	SP	UL
Pyrrhula pyrrhula	PYRPYR	PT/SP	UL
Pyrrhocorax pyrrhocorax	PYRRHO	PT/SP	F
Regulus ignicapilla	REGIGN	PT/SP	F
Regulus regulus	REGREG	PT/SP	F
Remiz pendulinus	REMPEN	PT/SP	UL
Saxicola rubetra	SAXRUB	PT/SP	UL
Saxicola torquatus	SAXTOR	PT/SP	UL
Serinus citrinella	SERCIT	SP	F
Serinus serinus	SERSER	PT/SP	AL
Sitta europaea	SITEUR	PT/SP	F
Sturnus unicolor	STUUNI	PT/SP	AL
Sylvia cantillans	SYLCAN	PT/SP	F
Sylvia communis	SYLCOM	PT/SP	UL
Sylvia conspicillata	SYLCON	PT/SP	UL
Sylvia hortensis	SYLHOR	PT/SP	F
Sylvia melanocephala	SYLMEL	PT/SP	F
Sylvia undata	SYLUND	PT/SP	UL
Turdus merula	TURMER	PT/SP	F
Turdus philomelos	TURPHI	PT/SP	F
Turnix sylvaticus	TURSYL	SP	F
Turdus torquatus	TURTOR	PT/SP	F

Table 5: R^2 of the ordinary least square (OLS) models and Nagelkerke pseudo-R^2 of the non-spatial components of the simultaneous autoregressive models (AR), for each taxonomic group at the grain size of 10 km x 10 km.

Model	Amphibians		Reptiles		Passerines	
	OLS	AR	OLS	AR	OLS	AR
M_{C}	0.165	0.165	0.098	0.095	0.331	0.328
M_{T}	0.058	0.050	0.174	0.171	0.291	0.269
M_{H}	0.150	0.123	0.075	0.056	0.132	0.119
M_{CT}	0.179	0.165	0.205	0.177	0.351	0.344
M_{CH}	0.221	0.211	0.183	0.151	0.368	0.359
M_{TH}	0.181	0.151	0.220	0.208	0.324	0.280
M_{CTH}	0.232	0.212	0.235	0.217	0.380	0.363

Table 6: Partial Regressions of the non-spatial components of the simultaneous autoregressive models, for each taxonomic group at the grain size of 10 km x 10 km.

Model	Amphibians		Reptiles		Passerines	
	Partial R^2	% of R^2	Partial R^2	% of R^2	Partial R^2	% of R^2
M_{CT}						
Climate	0.1146	69.4%	0.0062	3.5%	0.0748	21.7%
Topographic	0.0000	0.01%	0.0817	46.1%	0.0163	4.7%
Mixed	0.0502	30.4%	0.0891	50.3%	0.2527	73.5%
M_{CH}						
Climate	0.0881	41.7%	0.0947	62.7%	0.2398	66.8%
Habitat	0.0464	22.0%	0.0554	36.7%	0.0315	8.8%
Mixed	0.0767	36.3%	0.0006	0.4%	0.0877	24.4%
M_{TH}						
Topographic	0.0274	18.2%	0.1513	72.9%	0.1601	57.3%
Habitat	0.1003	66.5%	0.0366	17.6%	0.0102	3.7%
Mixed	0.0228	15.1%	0.0195	9.4%	0.1089	39.0%
M_{CTH}						
Climate	0.0609	28.7%	0.0089	4.1%	0.0830	22.9%
Topographic	0.0002	0.1%	0.0655	30.2%	0.0033	0.9%
Habitat	0.0466	22.0%	0.0392	18.1%	0.0185	5.1%
Mixed	0.1037	49.0%	0.1026	47.4%	0.2575	71.0%

B Supplementary material for chapter 3

Supplementary note

Here we show, in greater detail than in the main text, that sensitivities (σ) and affinities (h) are related. If one assumes full habitat conversion ($A - a = 0$ and $a = A$), and that species have maximum affinity for the native habitat, $h_1 = 1$, the affinity of a species group to the habitat of type *j*, can be derived with equation (3) in the main text:

$$\varepsilon(a) = \frac{S(A,0) - S(0,A)}{S(A,0)} = 1 - \left(\frac{h_j\,A}{A}\right)^z = 1 - h_j^z. \tag{1}$$

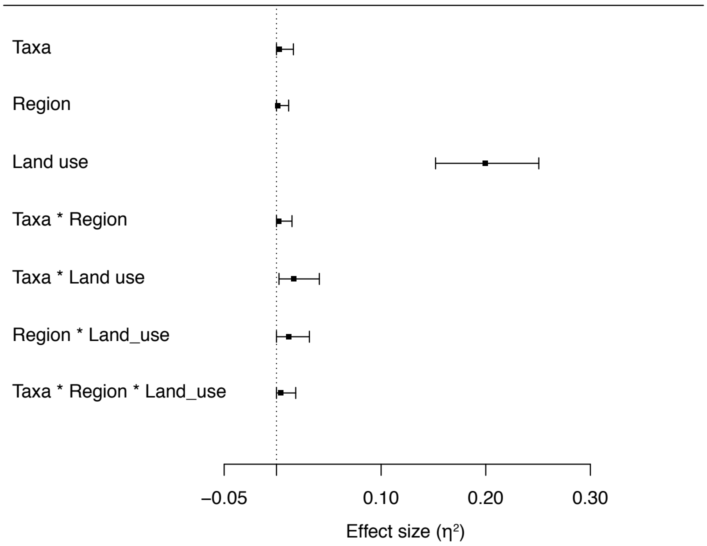
Knowing that, σ_j equals ε (equation (3)) at the plot scale when the native habitat is fully converted to habitat *j* (i.e., $a = A$):

$$\sigma_j = 1 - h_j^z. \tag{2}$$

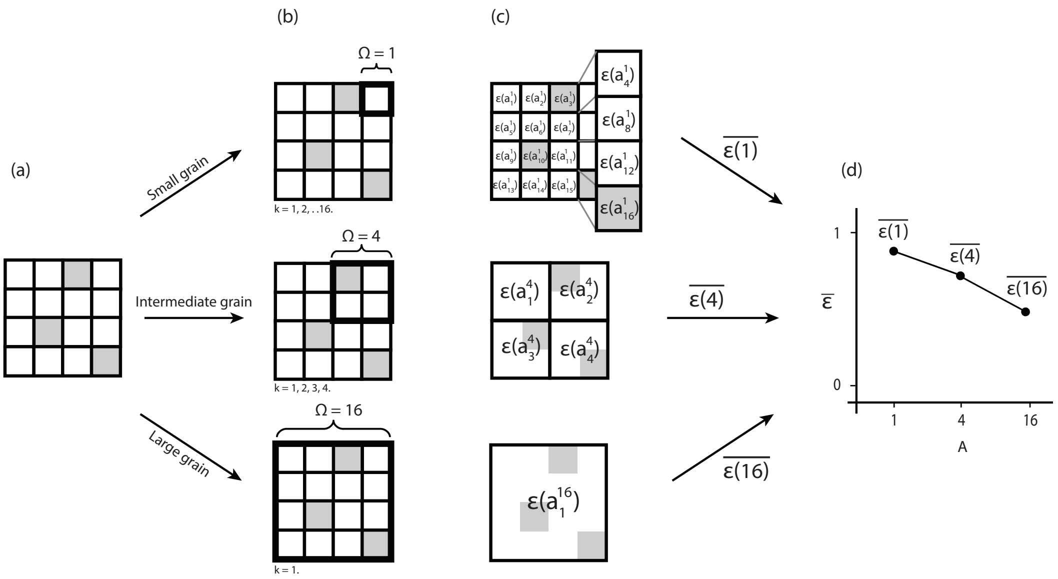
Thus, it is straightforward to show that:

$$h_j = (1 - \sigma_j)^{1/z}\,. \tag{3}$$

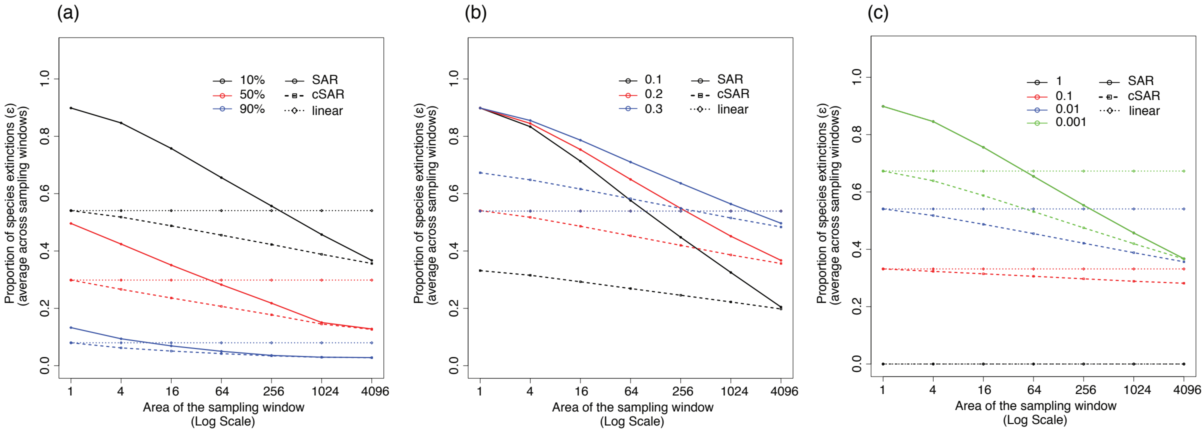
Supplementary Figures



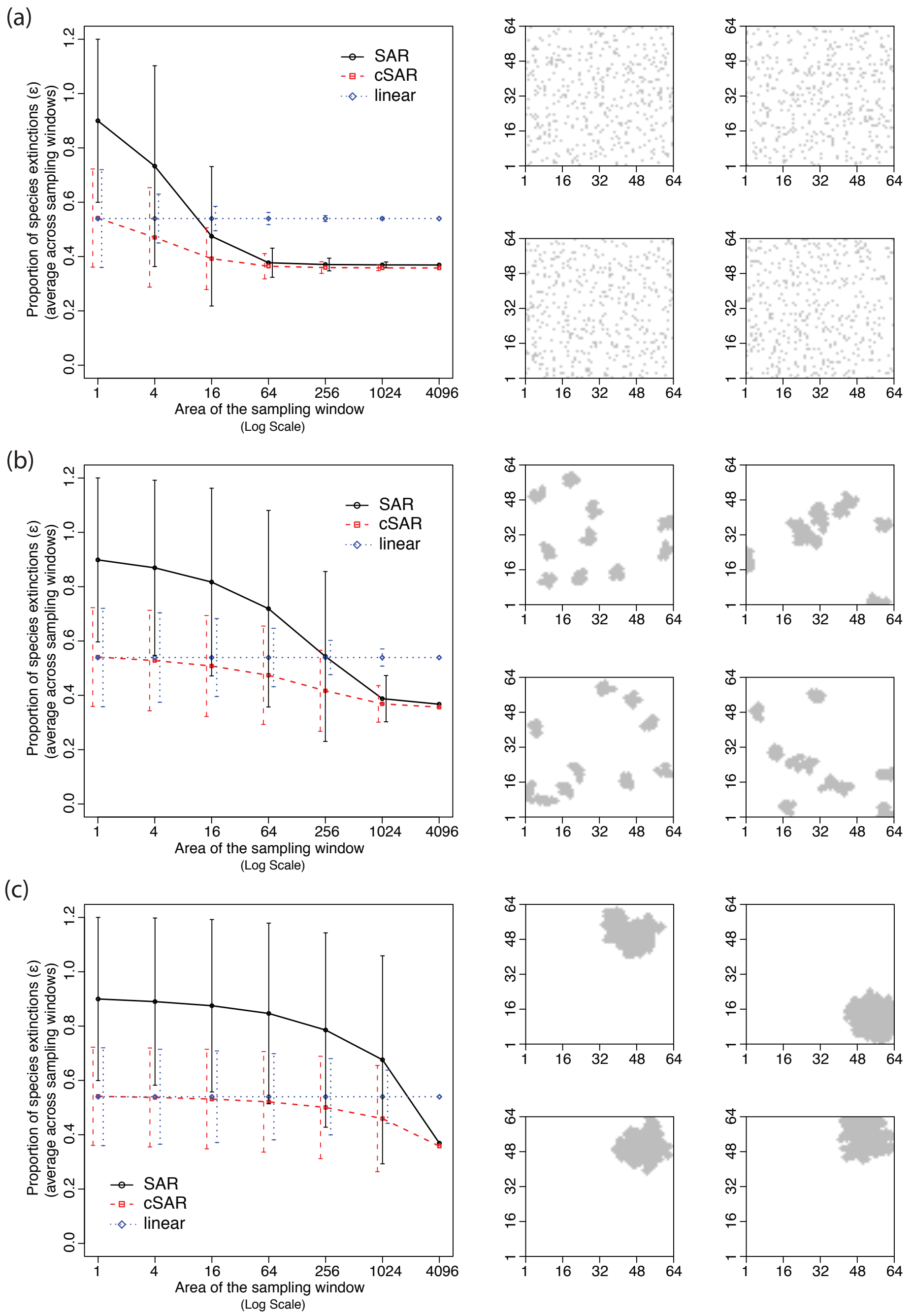
Supplementary Figure S1. Effect size (eta squared - η^2) and their confidence intervals (95% CIs) for the different categorical variables (i.e., taxa, region and land use) and their interactions analysed with a three-way ANOVA (N=730).



Supplementary Figure S2. Scheme exemplifying how the simulated landscapes were sampled to calculate the average proportion of species extinctions $\overline{\varepsilon(\Omega)}$, at each sampling grain, Ω. (**a**) potential configuration of a simulated landscape, illustrated for a 4 x 4 = 16 grid, with white squares corresponding to human-modified habitat and grey squares to the native habitat. (**b**) three different sampling grains: at the small sampling grain, sampling window *k* is only comprised of 1 cell $(\Omega = 1, N(\Omega) = 16)$, at the intermediate sampling grain, sampling window k is comprised of 4 cells $(\Omega = 4, N(\Omega) = 4)$ and at the large sampling grain, there is only one sampling window k and comprises all cells $(\Omega = 16, N(\Omega) = 1)$.(**c**) For a given model (see Methods), species extinctions, $\varepsilon(a_k^{\Omega})$, were calculated for each sampling window *k* of size Ω in the landscape (**d**) At each sampling grain, the projections of each sampling window were averaged to obtain the overall fraction of species going extinct in the landscape, where $\overline{\varepsilon(\Omega)} = \frac{\sum_k \varepsilon(a_k^{\Omega})}{N(\Omega)}$.



Supplementary Figure S3. Proportion of species extinctions (ε) in the simulated landscape after habitat conversion given by the linear, classic SAR and the countryside SAR. When varying **(a)** amount of native habitat left in the landscape (when z=0.2 and h_2=0.01), **(b)** the z-value (for 10% habitat remaining and h_2=0.01) and **(c)** species sensitivity for the modified habitat (for 10% habitat remaining and z=0.2). For all scenarios, h_1=1 for the native habitat. Points corresponds to the average number of species (across 1000 simulations) found in all sampling units of a given sample grain.



Supplementary Figure S4. Proportion of species extinctions (ε) in the simulated landscape after 90% habitat conversion given by the linear, classic SAR and the countryside SAR (z=0.2; h_1=1, h_2=0.01). When varying **(a-c)** the degree of fragmentation of the landscape after habitat conversion. Right panels show examples of the configuration of a simulated landscape to the different degrees of fragmentation, with white squares corresponding to human-modified habitat and grey squares to the native habitat. For all models, z = 0.2, with h_1=1 for the native habitat and h_2 = 0.01 for the modified habitat. Error bars indicate for each model, the standard deviation of the fraction of species remaining at a given sample grain.

Supplementary tables

Supplementary Table S1. Complete list of local sensitivities (σ - sigma) values. A total of 730 pairwise comparisons across two taxonomic groups (plants and birds), two broad ecological regions (tropical and temperate), and five different human-modified habitats (annual crops, managed forest, permanent crops, pastures and urban) were retrieved from the literature. Studies ('Source 2') were considered if they provided data on species richness on both a native habitat and at least one human-modified habitat. For several studies, more than one possible pairwise comparisons was reported.

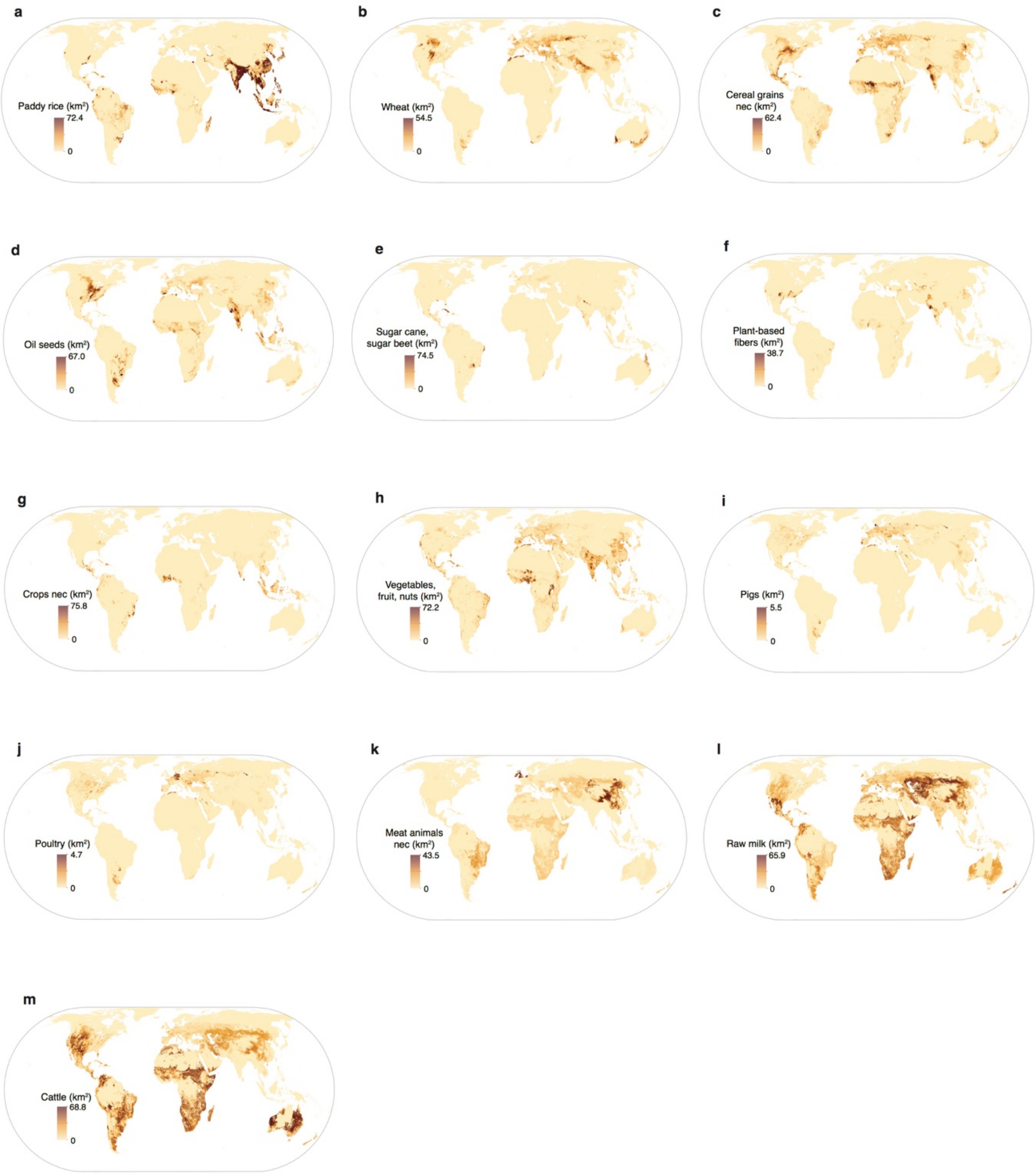
(*This table is provided in the cd attach to the dissertation*)

Supplementary Table S2. Average affinity values (*h*'s) for the different habitats and regions of the world.

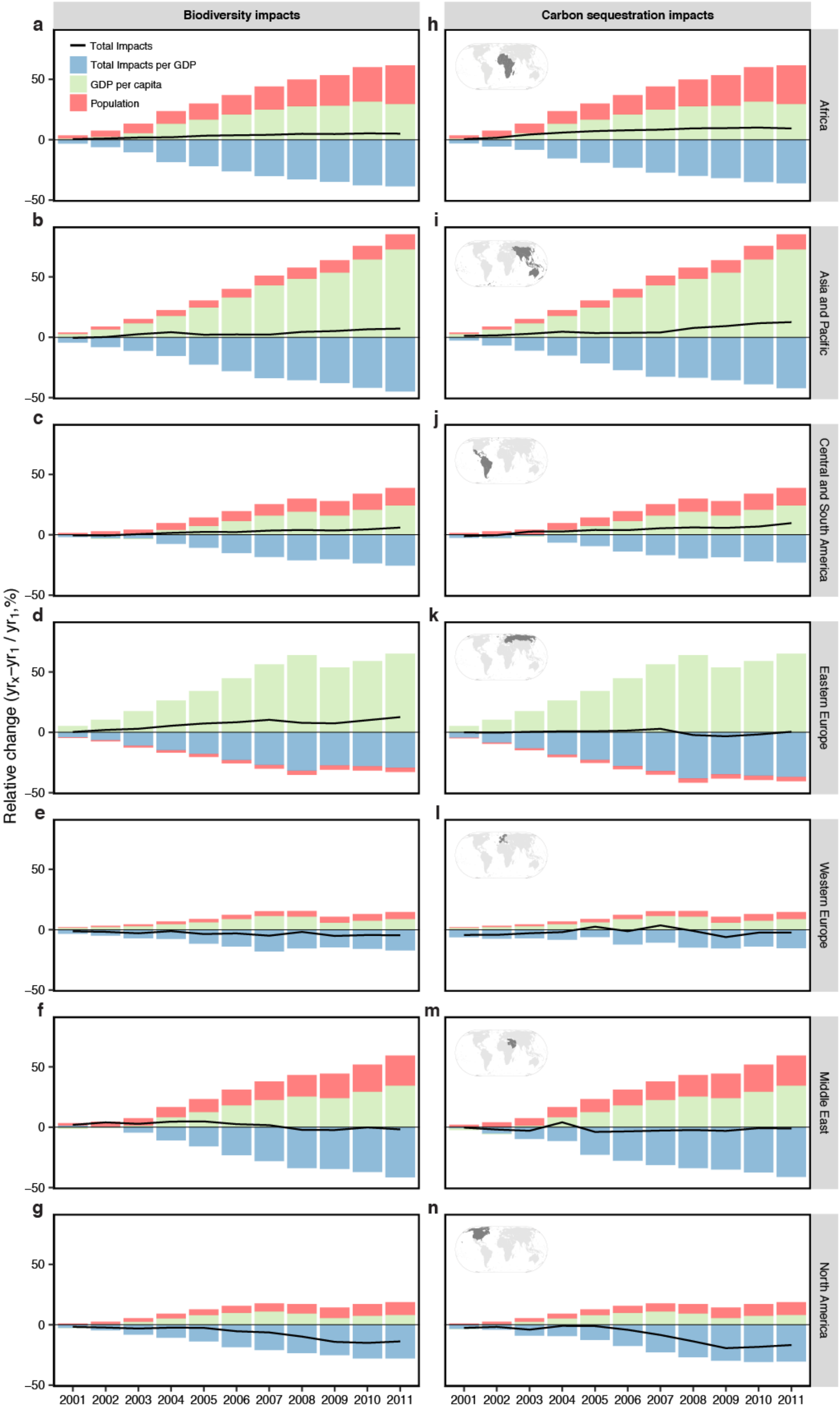
	Tropical	Temperate
Annual crops	0.0229	0.0150
Permanent crops	0.0206	0.0219
Pastures	0.0294	0.2999
Managed Forest	0.2365	0.3584
Urban	0.0209	0.0610

C. Supplementary material for chapter 4

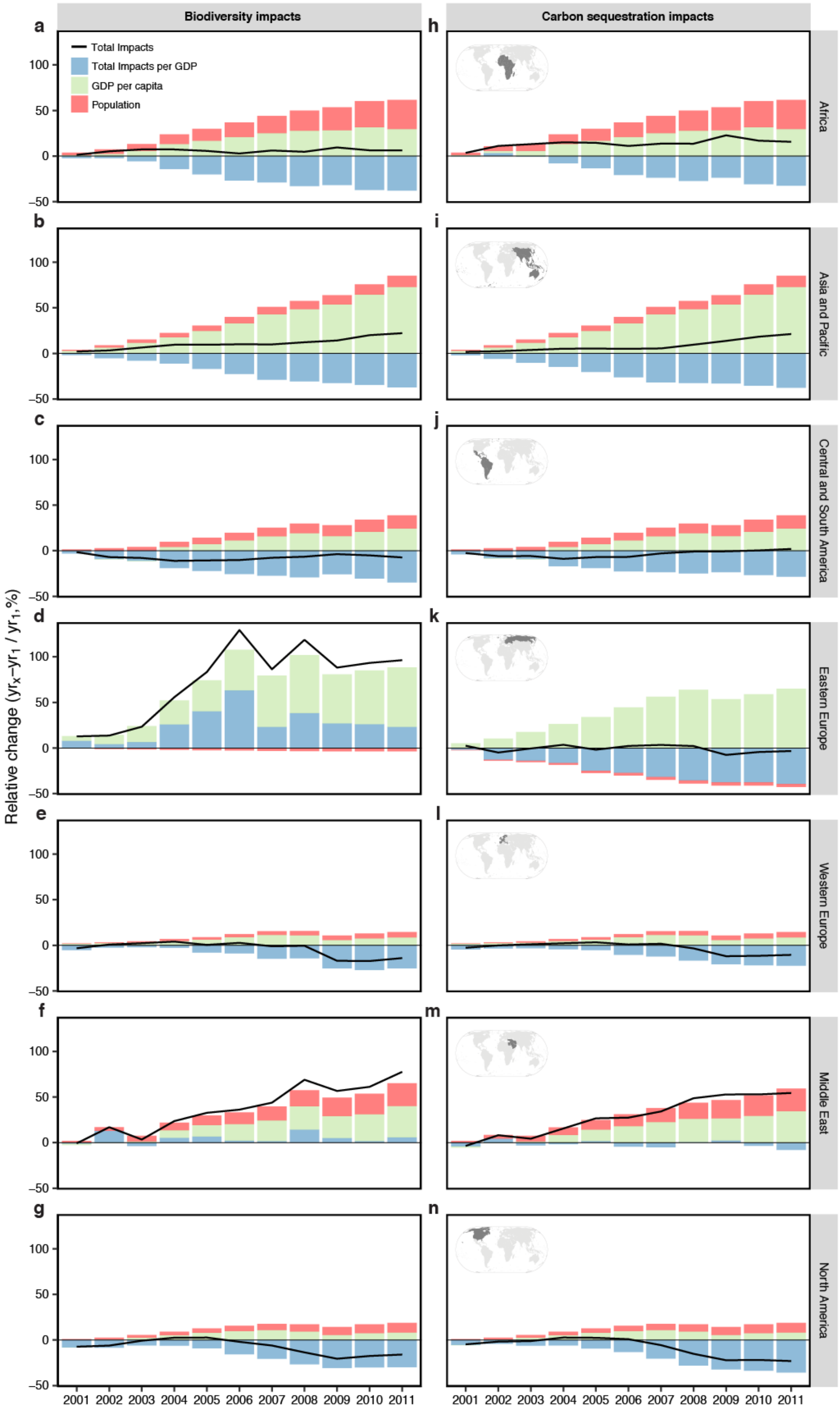
Extended data



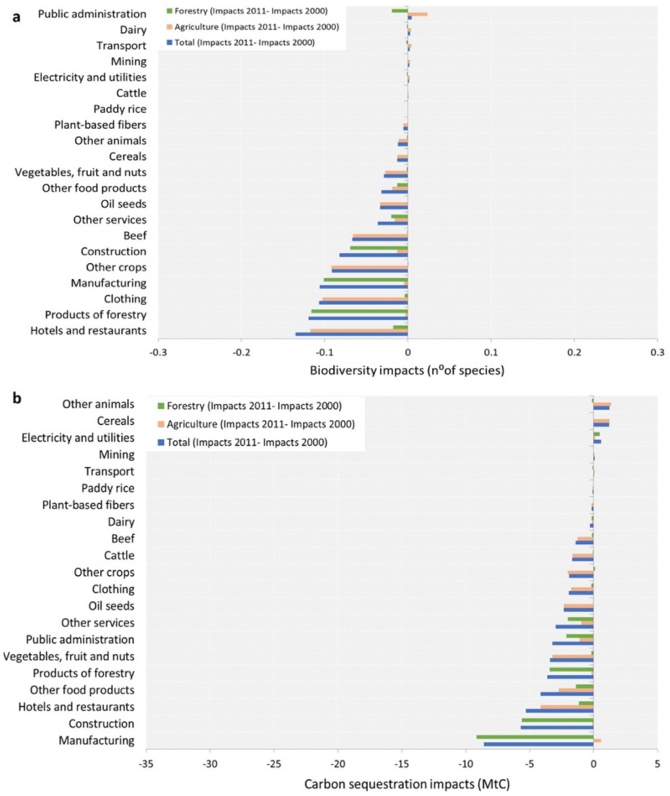
ED Figure 1 - Land use maps (**a**-**m**), in km^2, for the non-fodder crops, fodder crops (raw milk, cattle meat, pig meat, poultry and other meat), and permanent pastures (raw milk, cattle meat, other meat) layers at 5 arc min resolution (nec = not elsewhere classified).



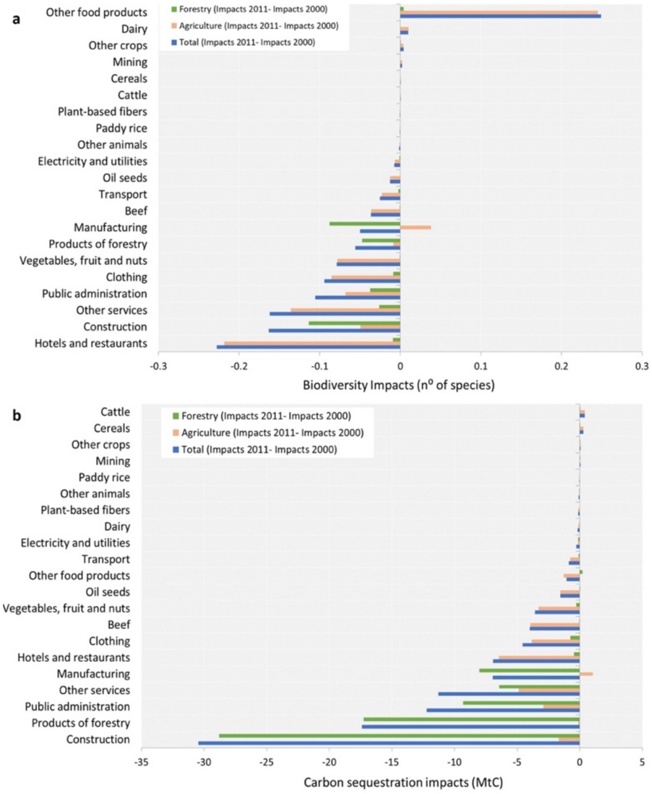
ED Figure 2 - Decomposition of impacts from agricultural and forestry activities on biodiversity (**a**-**g**) and carbon sequestration (**h**-**n**) into their immediate drivers for 7 world regions.



ED Figure 3 - Decomposition of impacts from consumption activities on biodiversity (**a**-**g**) and carbon sequestration (**h**-**n**) into their immediate drivers for 7 world regions.



ED Figure 4 - Sectoral disaggregation of the change in impacts between 2011 and 2000 on a) biodiversity (**a**; number of bird species) and carbon sequestration (**b**; MtC per year) in Western Europe.



ED Figure 5 - Sectoral disaggregation of the change in impacts between 2011 and 2000 on a) biodiversity (**a**; number of bird species) and carbon sequestration (**b**, MtC per year) in North America.

ED Table 1 - Impending bird extinctions (species numbers) due to domestic consumption and international trade between world regions, in 2000 and 2011. The grey cells indicate the impacts associated with domestic consumption. In the rows the impacts associated with the exports to other world regions are represented and in the columns the impacts associated with the imports from each region. Summing over the rows provides the total production impacts of a region, summing over the columns the total consumption impacts of a region.

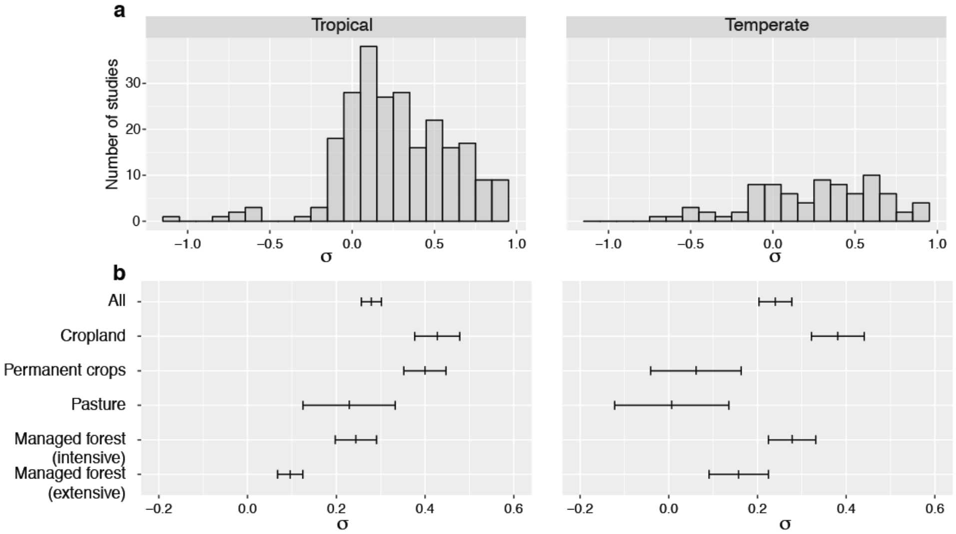
	Western Europe	Eastern Europe	Middle East	North America	Asia and Pacific	Africa	Central and South America
2000							
Western Europe	0.090	0.001	0.002	0.004	0.003	0.001	0.001
Eastern Europe	0.018	0.091	0.006	0.003	0.014	0.001	0.001
Middle East	0.010	0.001	0.093	0.004	0.005	0.002	0.001
North America	0.024	0.002	0.010	0.335	0.055	0.004	0.027
Asia and Pacific	1.460	0.299	0.439	1.642	19.022	0.145	0.238
Africa	2.315	0.191	0.417	0.563	0.711	14.137	0.150
Central and South America	2.083	0.215	0.428	2.179	1.127	0.179	20.733
2011							
Western Europe	0.084	0.003	0.002	0.003	0.004	0.002	0.001
Eastern Europe	0.019	0.082	0.019	0.005	0.019	0.005	0.001
Middle East	0.008	0.003	0.089	0.003	0.007	0.004	0.001
North America	0.016	0.003	0.012	0.253	0.080	0.005	0.025
Asia and Pacific	1.119	0.319	0.570	0.999	21.332	0.296	0.272
Africa	1.902	0.323	0.699	0.630	1.303	14.331	0.234
Central and South America	1.996	0.746	1.089	2.080	2.836	0.738	19.065

ED Table 2 - Carbon sequestration lost (MtC) due to international trade between world regions, in 2000 and 2011. The grey cells indicate the impacts associated with domestic consumption. In the rows the impacts associated with the exports to other world regions and in the columns the impacts associated with the imports from each region. Summing over the rows provides the total production impacts of a region, summing over the columns the total consumption impacts of a region.

	Western Europe	Eastern Europe	Middle East	North America	Asia and Pacific	Africa	Central and South America
2000							
Western Europe	185.549	4.374	6.280	8.013	9.816	2.790	2.205
Eastern Europe	43.526	293.921	10.516	7.994	33.127	1.528	1.644
Middle East	1.287	0.186	18.139	0.412	0.538	0.180	0.108
North America	17.751	1.269	4.924	302.099	38.704	1.354	16.062
Asia and Pacific	56.056	11.511	16.702	64.446	998.190	7.134	9.769
Africa	59.098	4.234	9.140	13.034	20.568	247.921	3.202
Central and South America	41.811	3.892	6.585	37.594	21.003	2.556	534.759
2011							
Western Europe	179.731	7.245	5.325	5.443	8.847	4.982	1.688
Eastern Europe	45.229	266.102	26.211	8.630	38.507	7.232	2.740
Middle East	1.022	0.409	17.800	0.295	0.676	0.335	0.088
North America	10.914	2.341	6.393	226.177	55.311	2.281	14.375
Asia and Pacific	47.700	13.915	23.023	43.643	1158.846	12.286	11.569
Africa	43.620	6.802	13.283	13.883	41.665	266.447	4.894
Central and South America	33.224	12.901	19.607	34.793	56.344	10.748	543.413

ED Table 3 - Affinity values (*h*) computed for the countryside species area relationship model used in the quantification of biodiversity impacts. Affinity values can be interpreted as the proportion of area of modified habitat that can be effectively used by a particular species group.

	Tropical	Temperate
Cropland	0.062	0.091
Permanent crops	0.077	0.731
Pastures	0.273	0.970
Managed Forest (intensive use)	0.247	0.196
Managed Forest (intensive and extensive use)	0.409	0.239



ED Figure 6 – Local scale sensitivity (σ) of species to the full conversion of native habitat into the human-modified habitat (i.e., the proportion of species disappearing at the plot-scale in human-modified habitats) in tropical and temperate regions. **a**, Distribution of σ found in the literature. **b**, range of σ values to the different land use activities. Error bars in **b** indicate standard errors.

Supplementary Methods and Supplementary Tables

(*This information can be found in the cd attach to the dissertation*)

D. Supplementary material for chapter 5

Supplementary Methods S1

In the twenty years analyzed (1990-2010), several land use trajectories were observed in Portugal (Historical trend in Tables SM1-SM3), which were projected to continue in the business-as-usual scenario (i.e., Pathway 0, Table SM1).

Table SM1. Expected transition matrix for the land uses in Portugal following Pathway 0 between 2010 and 2050. In the rows the changes in area projected to occur in each land use due to the transition to (-) or from (+) other land uses are represented. Summing over the row provides the change in area of each land use between the year 2010 and the year 2050 (i.e., 2010-2050 trend).

		Pathway 0					
	Historical Trend	Intensive Agriculture	Extensive Agriculture	Extensive Forest	Intensive Forest	Other Natural	2010-2050 Trend
Intensive Agriculture	-1.9	-	-7.4%				-7.4
Extensive Agriculture	-4.5	+2.1%	-	-11.2%		-5.6%	-14.67
Extensive Forest	-9.1		+14.6%	-	-19.8%	-11.9% +41.4%	+24.24%
Intensive Forest	+13.2			+48.0%	-	+7.0%	+54.95
Other Natural	+19.6		+10.5%	-60.0% +17.2%	-4.2%	-	-36.31

For example, the projected 7.4% loss in intensive agriculture is a result of losing each decade 1.9% (i.e., the historical trend) of area dedicated to this land use class in the previous decade, for the period of four decades (i.e., until year 2050). As there is no additional losses or gains in intensive agriculture area in the business-as-usual scenario, 7.4% is also how much the area of intensive agriculture changes between the year 2010 and the year 2050 (i.e., 2010-2050 trend). Such area was then assumed to change entirely to extensive agriculture, in cropland-grassland expansion, representing a gain of 2.1% in area of extensive agriculture. According to MAMAOT (2013), by 2010 extensive agriculture was showing a decreasing trend (4.5%), with 66% of such loss being allocated to extensive forest (i.e., new pine plantations) and 33% to other natural areas (i.e., natural areas that are not forest or agriculture areas and are not under any management regime) representing agricultural abandonment. Consequently, despite the gain in area from extensification of intensive agriculture areas, by 2050 we projected an overall 14.7% loss in extensive agriculture areas. In terms of forest, both the area of intensive and extensive forest were projected to increase by 2050. The increase in intensive forest area is a consequence of the expansion of eucalyptus plantations, as observed in the past 20 years, at the expense of extensive forest (90%) and other natural areas (10%), proportions that were kept for the business-as-usual scenario (MAMAOT, 2013). Despite the loss of extensive forest area by the intensification of forest plantations (19.8%) and by fire (11.9%) (Rosa *et .al*. 2011; MAMAOT, 2013), the area of extensive forest was projected to increase 24.4% by 2050. Such increase was due to new pine plantations from areas previously used in agriculture, the increasing agriculture abandonment and the rate of natural succession observed in Portugal in the past years. By 2050, we projected that more natural areas are being converted to forest as consequent of natural succession (60%), then being created by agricultural abonnement (10.5%) or fire events (17.2%), leading to a 36.3% decreased of the country's other natural areas.

Table SM2. Expected transition matrix for the land uses within Portugal following Pathway A between 2010 and 2050. In the rows the changes in area projected to occur in each land use due to the transition to (-) or from (+) other land uses are represented. Summing over the row provides the change in area of each land use between the year 2010 and the year 2050 (i.e., 2010-2050 trend).

		Pathway A					
	Historical Trend	Intensive Agriculture	Extensive Agriculture	Extensive Forest	Intensive Forest	Other Natural	2010-2050 Trend
Intensive Agriculture	-1.9	-------------------- Locked --------------------					0
Extensive Agriculture	-4.5		-	-22.7%		-11.3%	-34
Extensive Forest	-9.1		+29.5%	-		-12.3% +20.7%	+37.95
Intensive Forest	+13.2	-------------------- Locked --------------------					0
Other Natural	+19.6		+21.4%	-30.0% +17.8%		-	+9.17

The trends projected for the period 2010-2050 in Pathways A and B were obtained by modifying the historical trends (1990-2010) through a series of assumptions, in order to fit the storylines described in section 2.1. In Pathway A, both intensive agriculture and intensive forest were locked, meaning that their proportion on the landscape does not change from 2010 to 2050 (Table S2). Consequently, there is no projected increase of extensive agriculture area from the extensification of intensive agriculture areas, or decrease in extensive forest and other natural areas due to the expansion of eucalyptus plantations. We doubled the rate of loss in extensive agriculture compared to the business-as-usual scenario, as we expect the abandonment of less productive and marginal agriculture areas (section 2.1). However, we maintained the proportion of that rate that transitions to extensive forest (66%) and to other natural (33%), leading to a 34% decrease in the area of extensive agriculture by 2050. Furthermore, we assumed a decrease in the rate of natural succession, compared to business-as-usual scenario, as a result of management to maintain as other natural areas (section 2.1), which decreased the amount of other natural area projected to be converted to extensive forests. Despite that, and the losses by fire, we projected an increase in extensive forest as more pine plantations transitioned from extensive agriculture areas (29.5%) and no forest was intensified. As natural succession rate is influence by active management, the increase of other natural areas was kept stable (i.e., following the historical trend).

Table SM3. Expected transition matrix for the land uses within Portugal following Pathway B between 2010 and 2050. In the rows the changes in area projected to occur in each land use due to the transition to (-) or from (+) other land uses are represented. Summing over the row provides the change in area of each land use between the year 2010 and the year 2050 (i.e., 2010-2050 trend).

		Pathway B					
	Historical Trend	Intensive Agriculture	Extensive Agriculture	Extensive Forest	Intensive Forest	Other Natural	2010-2050 Trend
Intensive Agriculture	-1.9	-	-50.0%				-50
Extensive Agriculture	-4.5	+14.3%	-			-2.8%	+11.47
Extensive Forest	-9.1			-		-6.0% +20.7%	+14.75
Intensive Forest	13.2			-------------------------------------- Locked --------------------------------------			0
Other Natural	19.6		+5.3%	-30.0% +8.6%		-	-16.07

In Pathway B, similarly to Pathway A, intensive forest was locked, and no decrease in extensive forest and other natural areas due to the expansion of eucalyptus plantations was allowed (Table S3). Here, we assumed a 50% reduction in the area of intensive agriculture, which was then assumed to change entirely to extensive agriculture, in cropland-grassland expansion. Leading to an increase of 14.3% in area of extensive agriculture. With multifunctionality in mind, loss of extensive agriculture due to the expansion of extensive forest (i.e., new pine plantations) was locked. While the loss by agriculture abandonment (i.e., conversion to other natural areas) was decrease by half, as some less productive and marginal agriculture areas prevailed. Consequently, by 2050, we projected an increase in the country's extensive agriculture area (11.5%). Here, extensive forest area was only projected to increase 14.8% by 2050 (lower increase of all scenarios). While we assumed a 50% reduction in the rate of loss of extensive forest (compare to the rate in the business-as-usual scenario) as a result of fire. We also locked the transition from extensive agriculture and assume, as in Pathway A, a decrease in the rate of natural succession, compared to the business-as-usual scenario. This again decreased the amount of other natural area projected to be converted to extensive forests (60% in Pathway 0 *vs* 30% in Pathways A and B). Finally, we projected that by 2050, more natural areas were being converted to forest as consequent of natural succession (30%), then being created by agricultural abonnement (5.3%) or fire events (8.6%). Leading to a 16.1% decreased of the country's other natural areas.

Supplementary Methods S2

Note that affinity values (h_{ij}) reflect the habitat affinity of a species group to human-modified habitat of type *j* compared to its native habitat. If one assumes full habitat conversion ($A_1 - A_j$ = 0 and A_j = A_1), and that species have maximum affinity for the native habitat, h_1 = 1 (which is just a matter of standardization), then according with the cSAR, the change in species richness between the original native habitat $S(1)$ and the modified habitat $S(j)$ is estimated as:

$$\frac{S(j)}{S(1)} = \left(\frac{h_1\left(A_1 - A_j\right) + h_j A_j}{h_1 A_1}\right)^z \tag{1}$$

$$= \left(\frac{h_j A_j}{h_1 A_1}\right)^z \tag{2}$$

$$= \left(\frac{h_j}{h_1}\right)^z, \tag{3}$$

where the habitat affinity to a human-modified habitat of type *j* can be expressed as the ratio of species richness before and after habitat modification powered by the SAR-slope:

$$h_j = \left(\frac{S(j)}{S(1)}\right)^{\frac{1}{z}}, \tag{4}$$

and $\frac{S(j)}{S(1)}$ represent the proportion of species remaining after habitat conversion and can be estimated from local data studies (i.e. studies carried out at plot size scale).

To estimate the habitat affinities for intensive agriculture and intensive forest we first selected local studies across the Iberian Peninsula that provided data on bird species richness on both native habitat $S(1)$ and at least one of the human-modified habitat of interest $S(j_{int})$ (i.e., when *j* is an agriculture or forest habitat and intensively used; Table S4). We then calculated $h_{ij_{int}}$ using the mean response of species to the two different intensively used human-modified habitats and the countryside SAR parameters calculated by Martins et al (2014), assuming that species affinities would decrease proportionally to the decrease in species observed in local studies where intensive and native landscapes were sampled:

$$h_{ij_{int}} = h_{ij} * \left(\frac{1}{n} \sum_{i=1}^{n} \frac{S(j_{int})}{S(1)} \right) , \qquad (5)$$

where n is the number of studies.

Supplementary Tables

Table S1. Reclassification of the CORINE land cover classes into the five land use classes used to project future changes in land use until the year 2050.

Original CORINE Land Cover Class	CLC_ID	Land use classes
(source: Rosa et al. 2011)	Eucalyptus	Intensive Forest
(source: Rosa et al. 2011)	Other forest	Extensive Forest
Non-irrigated arable land	211	Extensive Agriculture
Permanently irrigated land	212	Intensive Agriculture
Rice fields	213	Intensive Agriculture
Vineyards	221	Intensive Agriculture
Fruit trees and berry plantations	222	Intensive Agriculture
Olive groves	223	Intensive Agriculture
Pastures	231	Extensive Agriculture
Annual crops associated with permanent crops	241	Extensive Agriculture
Complex cultivation patterns	242	Extensive Agriculture
Land principally occupied by agriculture, with significant areas of natural vegetation	243	Extensive Agriculture
Agro-forestry areas	244	Extensive Agriculture
Broad-leaved forest	311	Intensive Forest
Coniferous forest	312	Extensive Forest
Mixed forest	313	Extensive Forest
Natural grasslands	321	Other Natural
Moors and Heathlands	322	Other Natural
Sclerophyllous vegetation	323	Other Natural
Transitional woodland-shrub	324	Other Natural
Sparsely vegetated areas	333	Other Natural
Burnt areas	334	Other Natural

Table S2. Parameters used in the cSAR model to project biodiversity by 2050 in Portugal. h_{Aext}, h_{Aint}, h_{ON}, h_{Fext} and h_{Fint}, represent the affinity of the species groups for extensive agriculture, intensive agriculture, other natural, extensive forest and intensive forest, respectively; *c* and *z* represent the model parameters of cSAR.

	c	z	h_{Aext}	h_{Aint}	h_{ON}	h_{Fext}	h_{Fint}
Agricultural species	1.84	0.101	1	0.06	0.604	0.305	0.02
Forest species	1.86	0.126	5.91E-05	6.09E-06	0.007	1	1.03E-01
Other species	0.67	0.162	0.2	0.20	1	0.362	0.06

Table S3. Change in alpha (local) and gamma (national) species richness (*Sp.*- in numbers; *%* - in percentage) of the different species groups between the baseline 2010 and the different pathways.

	Alpha															
	Agricultural sp.				*Other sp.*				*Forest sp.*				*Total sp.*			
2050-2010	*Sp.*		*%*		*Sp.*		*%*		*Sp.*		*%*		*Sp.*		*%*	
	Mean	SD	Mean	SD	Mean	SD	Mean	SD	Mean	SD	Mean	SD	Mean	SD	Mean	SD
Pathway 0	-0.14	0.09	-1.29	0.84	-0.21	0.24	-1.84	2.11	0.65	0.62	4.35	4.40	0.30	0.64	0.82	1.72
Pathway A	-0.16	0.09	-1.47	0.78	0.13	0.16	1.20	1.45	0.66	0.33	4.41	2.50	0.63	0.41	1.70	1.15
Pathway B	0.02	0.07	0.17	0.67	-0.04	0.13	-0.33	1.17	0.27	0.26	1.81	1.79	0.25	0.26	0.69	0.70

	Gamma							
	Agricultural sp.		*Other sp.*		*Forest sp.*		*Total sp.*	
2050-2010	*Sp.*	*%*	*Sp.*	*%*	*Sp.*	*%*	*Sp.*	*%*
Pathway 0	-0.26	-1.17	-0.67	-1.99	1.25	3.26	0.32	0.34
Pathway A	-0.30	-1.35	0.42	1.25	1.35	3.53	1.48	1.57
Pathway B	0.02	0.08	-0.19	-0.57	0.56	1.47	0.39	0.40

Table S4. List of bird species' local sensitivities (σ - sigma) values for intensively used habitats. Studies were considered if they provided data on species richness on both a native habitat and at least one human-modified habitat intensively used.

Source	*Region*	*Habitat*	*Sigma*
Suárez-Seoane et al. 2002	Spain	Cropland	0.465
Suárez-Seoane et al. 2002	Spain	Cropland	0.241
Chaudhary et al. 2015	Spain	Cropland	0.524
Suárez-Seoane et al. 2002	Spain	Managed forest, intensive	0.581
Suárez-Seoane et al. 2002	Spain	Managed forest, intensive	0.483
Calvino-Cancela 2013	Spain	Managed forest, intensive	0.594
Calvino-Cancela 2013	Spain	Managed forest, intensive	0.563
Calvino-Cancela 2013	Spain	Managed forest, intensive	0.625
Proença et al. 2010	Portugal	Managed forest, intensive	0.350

E. Curriculum Vitae

Inês Santos Martins

PERSONAL INFORMATION

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EDUCATION/ACADEMIC EMPLOYMENT

Current position

2013-present	***Doctoral student (under the supervision of Henrique M. Pereira)*** German Centre for Integrative Biodiversity Research (iDiv) Martin Luther University Halle-Wittenberg (MLU), Germany *transferred in 2014 from* Centre of Environmental Biology, Faculty of Sciences of the University of Lisbon, Portugal.

Previous positions

2011-2012	***Research Fellow*** Centre of Environmental Biology, Faculty of Sciences of the University of Lisbon, Portugal.
2009-2011	***M.Sc. Ecology and Environmental Management*** Faculty of Sciences, University of Lisbon, Portugal.
2006-2009	***B.Sc. in Environmental Biology – Terrestrial variant*** Faculty of Sciences, University of Lisbon, Portugal.

Other employment

2009	**GIS assistant (internship)** Bio3, Studies and projects in biology and natural resources valorization Lda.

FELLOWSHIPS AND GRANTS

2013-2015	PhD fellowship from Fundação para a Ciência e a Tecnologia, Portugal. The application included a research proposal. The studentship was awarded for 4 years. It was eventually suspended following my stay in the German Centre for Integrative Biodiversity Research (iDiv), as a result of my supervisor's new position at iDiv.

ACADEMIC ACTIVITIES

Reviewing:

2018	Ecography

Teaching:

2014-2017	Teaching Assistant, Spatial Ecology course for the master program, taught by Prof. Henrique Pereira at Martin Luther University of Halle-Wittenberg.
2014; **2017**	Teaching Assistant, Nature Conservation course for the master program, taught by Dr. Henrique Pereira at Martin Luther University of Halle-Wittenberg.

Supervising:

February 2018	Pascal Schnitker (6 weeks internship)

Involvement in multi-party projects:

2017-ongoing	Biodiversity and Ecosystem Services Scenarios using Shared Socio-economic Pathways for IPBES. IPBES Global Assessment on Biodiversity and Ecosystem Services.
2015-2016	Exploring transition pathways to sustainable, low carbon societies – PATHWAYS Project. EU-Seventh Framework Program (FP7).
2014-**2015**	DEvelopment of a System of Indicators for a Resource efficient Europe – DESIRE Project. EU-Seventh Framework Program (FP7).
2011-**2012**	Biodiversity Monitoring in Environmental Assessments - MoBiA Project. PTDC/AAC-AMB/114522/2009.

Other activities:

2018	Member of the organization committee of the iDiv Summer School 2018.
2014-2018	Member of the graduate school of the German Centre for Integrative Biodiversity Research (yDiv).
2015	Member of the organization committee of the 1st iDiv conference.

Halle (Saale), den 16.07.2018

Inês Martins

F. List of publications and conference participations

Publications of the dissertation

- **Martins I.S.**, Proença V., Pereira H.M. (2014) The unusual suspect: Land use is a key predictor of biodiversity patterns in the Iberian Peninsula. *Acta Oecologica*, 61, 41–50.
- **Martins, I.S.** & Pereira, H.M. (2017) Improving extinction projections across scales and habitats using the countryside species-area relationship. *Scientific Reports*, 7, 12899.
- Marques, A., **Martins I.S**., Pereira H.M., et al. *to be resubmitted to Nature Ecology and Evolution*. Trends on higher land-use efficiency insufficient to mitigate impacts on nature from population and consumption growth.
- **Martins, I.S**., Navarro, L.M., Rosa, I.M., & Pereira, H.M. *in preparation*. Winners and losers: How different pathways for a sustainable future affects species communities.

Peer-reviewed publications

- **Martins, I.S**., Rosa, I.M., & Pereira, H.M. *in preparation*. Projecting impacts of global land-use scenarios on biodiversity change across scales and species groups.
- Pereira, H.M., Rosa, I.M., […] **Martins, I.S**., et al. *in preparation*. A multimodel comparison of biodiversity historical trends and future scenarios with the shared socio-economic pathways
- Shin, Y.J., Arneth A., Midgley G.F., […] **Martins, I.S**., et al. (2018) Plausible futures of nature, its contributions to people and their good quality of life. In: IPBES Global Assessment on Biodiversity and Ecosystem Services. [Contributing author]
- Kim, H., Rosa, I.M.D., Alkemade, R., […] **Martins, I.S**., et al. (2018) A protocol for an intercomparison of biodiversity and ecosystem services models using harmonized land-use and climate scenarios. *bioRxiv*, 300632.
- Cameron, E.K., **Martins, I.S.**, Lavelle, P., et al. (2018) Global gaps in soil biodiversity data. *Nature Ecology & Evolution.* 1.
- Keil, P., Pereira, H.M., Cabral, J.S., Chase, J.M., May, F., **Martins, I.S**., & Winter, M. (2017) Spatial scaling of extinction rates: Theory and data reveal nonlinearity and a major upscaling and downscaling challenge. *Global Ecology and Biogeography*, 27, 2–13.
- Pereira, H. M., Navarro, L. M. & **Martins, I.S**. (2012) Global Biodiversity Change: The Bad, the Good, and the Unknown. *Annu. Rev. Environ. Resourc.* 37, doi:10.1146/annurev-environ-042911-093511
- Pereira, H.M., Borda-de-Agua, L. & **Martins, I.S**. (2012) Geometry and scales in species-area relationships. *Nature* 482, doi:10.1038/nature10857

Technical reports

- **Martins, I.S**., Rosa, I.M., Zwartkruis, J., Navarro, L.M., , Pereira, H.M. (2017) Exploring transition pathways to sustainable, low carbon societies (PATHWAYS): Challenges towards more biodiversity friendly landscapes (Policy brief).
- **Martins, I.S**., Navarro, L.M., Rosa, I.M., Pereira, H.M. (2016) Exploring transition pathways to sustainable, low carbon societies (PATHWAYS): The land use and biodiversity domain in the Portugal (D2.5, report 10).

- Hof, A.F., van Sluisveld, M.A.E., Carrara, S., DeCian, E., Köhler, J., **Martins, I.S**., Navarro, L.M., Oehler, P., Pereira, H.M., Pfluger, B., Rosa, I.M., Savvidou, G., Westhoek, H., van Vuuren, D.P., Zwartkruis, J. (2016) Exploring transition pathways to sustainable, low carbon societies (PATHWAYS): The land use and biodiversity domain in the Portugal (D1.3).
- Marques, A., **Martins I.S.**, Elshout, P., , Hilbers, J., Kastner, T., Eisenmenger, N., Fetzel, T., Plutzar, C., Theurl, M.C., Huijbregts, M.A.A, Erb, K., Pereira H.M. (2015) DEvelopment of a System of Indicators for a Resource efficient Europe (DESIRE): Integrated WP report with calculated biodiversity and ecosystem service impact indicators (Calculated biodiversity and ecosystem service impact indicators) (D7.3).
- Marques, A., Canelas, J., **Martins I.S.**, Huijbregts, M.A.A, Hilbers, J., Eisenmenger, N., Theurl, M.C., Erb, K., Pereira H.M. (2014) DEvelopment of a System of Indicators for a Resource efficient Europe (DESIRE): Interim report on calculation of biodiversity and ecosystem impacts (Calculation of biodiversity and ecosystem services impacts in an IO framework) (D7.2).

Invited talks and posters (selection)

- Martins, I.S., Marques, A., Pereira, H.M**.** (2018) Projecting impacts of global land-use scenarios on biodiversity change across scales and species groups. **5th European Congress for Conservation Biology (ECCB)**. Jyväskylä, Finland. 2018 (talk)
- Martins, I.S., Navarro, L.M., Rosa, M.D.I, Pereira, H.M. (2016) Biodiversity response to sustainable pathways in Portugal. **PATHWAYS – EEA (SOER 2020) workshop**, Copenhagen, Denmark. (talk)
- Martins, I.S., Navarro, L.M., Rosa, M.D.I, Pereira, H.M. (2016) Biodiversity response to sustainable pathways in Portugal. **2nd iDiv Conference**, Leipzig, Germany. (talk)
- Martins, I.S., Navarro, L.M., Rosa, M.D.I, Pereira, H.M. (2016) Biodiversity response to sustainable pathways in Portugal. **ARTS/TESS/PATHWAYS workshop**. Rotterdam, The Netherlands. (talk)
- Martins, I.S., Marques, A., Pereira, H.M. (2015) Using countryside species area relationship to quantify the impacts of land use on biodiversity. **27th International Congress for Conservation Biology (ICCB) , 4th European Congress for Conservation Biology (ECCB). Montpellier**, France. (talk)
- Martins, I.S., Pereira, H. M., Proença. V. (2013) Beyond area and climate: the effect of habitat diversity on species richness patterns at the Iberian Peninsula scale. **1st yDiv Symposium**, Leipzig, Germany. (poster)
- Martins, I.S., Pereira, H. M., Proença. V. (2013) Beyond area and climate: the effect of habitat diversity on species richness patterns at large spatial scales. **14º Encontro Nacional de Ecologia SPECO**/Encontro da Primavera APEP. Bragança, Portugal. (talk)

G. Authors' contributions

Chapter 2

Martins, I.S., Proença, V., & Pereira, H.M. (2014) The unusual suspect: Land use is a key predictor of biodiversity patterns in the Iberian Peninsula. *Acta Oecologica*, 61, 41–50.

Design/Analysis: Martins, I.S. (80%), Proença, V. (10%),, Pereira H. M. (10%)

Writing: Martins, I.S. (70%), Proença, V. (20%), Pereira H. M. (10%)

Chapter 3

Martins, I.S. & Pereira, H.M. (2017) Improving extinction projections across scales and habitats using the countryside species-area relationship. *Scientific Reports*, 7, 12899.

Design/Analysis: Martins, I.S. (80%), Pereira H. M. (20%)

Writing: Martins, I.S. (70%), Pereira H. M. (30%)

Chapter 4

Marques, A., **Martins I.S.**, Kastner, T., Plutzar, C., Theurl, M.C., Eisenmenger, N., Huijbregts, M.A.A, Wood, R., Stadler, K., Bruckner, M., Canelas, J., Hilbers, J., Tukker, A., Erb, K., Pereira H.M. *to be resubmitted in Nature Ecology and Evolution*. Trends on higher land-use efficiency insufficient to mitigate impacts on nature from population and consumption growth.

Design/Analysis: Marques, A. (45%), Martins I.S. (25%), Kastner, T. (12.5%), Pereira H.M. (7.5%), Plutzar, C. (5%), Theurl, M.C.(5%), Eisenmenger, N., Huijbregts, M.A.A, Wood, R., Stadler, K., Bruckner, M., Canelas, J., Hilbers, J., Tukker, A., Erb, K., (corrections)

Writing: Marques, A. (60%), Pereira H.M. (20%), Martins I.S. (10%), Kastner, T. (5%), Plutzar, C. (5%), Theurl, M.C., Eisenmenger, N., Huijbregts, M.A.A, Wood, R., Stadler, K., Bruckner, M., Canelas, J., Hilbers, J., Tukker, A., Erb, K., (corrections)

Chapter 5

Martins, I.S., Navarro, L.M., Rosa, I.M., Pereira, H.M. *in preparation*. Winners and losers: How different pathways to a sustainable future affects species communities.

Design/Analysis: Martins, I.S. (75%), Rosa, I.M. (10%) , Navarro, L.M. (10%), Pereira H. M. (5%)

Writing: Martins, I.S. (75%), Rosa, I.M. (10%) , Navarro, L.M. (10%), Pereira H. M. (5%)

Halle (Saale), 16.07.2018

Ines Martins

H. Eigenständigkeitserklärung

Hiermit erkläre ich, dass die Arbeit mit dem Titel „Understanding species responses to habitat change across scales using the countryside species-area relationship“ bisher weder bei der Naturwissenschaftlichen Fakultät I Biowissenschaften der Martin-Luther-Universität Halle-Wittenberg noch einer anderen wissenschaftlichen Einrichtung zum Zweck der Promotion vorgelegt wurde.

Ferner erkläre ich, dass ich die vorliegende Arbeit selbstständig und ohne fremde Hilfe verfasst sowie keine anderen als die angegebenen Quellen und Hilfsmittel benutzt habe. Die den Werken wörtlich oder inhaltlich entnommenen Stellen wurden als solche von mir kenntlich gemacht.

Ich erkläre weiterhin, dass ich mich bisher noch nie um einen Doktorgrad beworben habe.

Halle (Saale), den 16.07.2018

Ines Martins