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Of food & fauna:  
investigating the relationship between global  
agricultural land use & biodiversity

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## **Abstract**

Agricultural land use dominates one third of the Earth's land surface and is the single biggest driver of biodiversity loss. Moreover, with a growing human population and a rising demand for resources, the impact of agricultural land use on biodiversity is projected to escalate. The main goal of this thesis was to gain a deeper understanding of the relationship between agricultural land use and biodiversity on a global scale. In approaching this goal, this thesis aims to bridge three main research gaps. First, while much research has addressed the effect of agricultural expansion on biodiversity, relatively little work has investigated the relationship between the many facets of agricultural intensification and biodiversity. Second, most studies on land use and biodiversity have assessed local to regional scale impacts, whereas few have assessed this relationship on a global scale. This gap is particularly critical in terms of predicting species richness – where environmental factors rather than human driven factors have traditionally been thought to be important in driving and predicting broad-scale patterns of biodiversity. Third, in light of growing future demand for resources, a better understanding is needed regarding the impact of future agricultural land use on biodiversity. This thesis made progress in bridging these research gaps by (i) mapping patterns of multiple metrics of land-use intensity and biodiversity, (ii) improving species-area relationships with the inclusion of land cover and land-use intensity metrics, and (iii) identifying highly biodiverse areas at risk under trajectories of potential future agricultural expansion and intensification. Patterns of land-use intensity metrics were heterogeneously distributed in areas of high biodiversity, suggesting that conservation research should include multiple intensity metrics in order to avoid underestimating biodiversity threat. Furthermore, results show land-use intensity was found to rival biomes in predicting global species richness, thus upgrading one of the most fundamental laws in ecology, and providing an improved understanding of broad-scale species richness patterns. Finally, areas most at-risk under potential future agricultural change were found to be widespread across Latin America and Sub-Saharan America. These results deliver crucial insights in proactively mitigating future potential conflicts in the nexus of biodiversity and land use. Overall, considering the great threat agriculture poses to biodiversity, this thesis highlighted the complexity and importance of land-use intensity in its relationship with biodiversity and uncovered highly biodiverse areas threatened by agricultural land use, both currently and in the future.





## **Zusammenfassung**

Die landwirtschaftliche Landnutzung dominiert ein Drittel der Erdoberfläche und ist der größte Einflussfaktor des Biodiversitätsverlustes. Zudem wird prognostiziert, dass sich mit wachsender Erdbevölkerung und zunehmendem Bedarf an Ressourcen der Einfluss der landwirtschaftlichen Landnutzung auf die Biodiversität massiv ausweiten wird. Das Hauptziel dieser Dissertation war es, ein tieferes Verständnis über die Beziehung zwischen landwirtschaftlicher Landnutzung und Biodiversität auf globaler Skala zu entwickeln. Um dieses Ziel zu erreichen möchte diese Dissertation eine Brücke über drei Forschungslücken schlagen. Erstens, während sich bereits viele Studien mit der Auswirkung der landwirtschaftlichen Expansion auf die Biodiversität beschäftigt haben, untersuchten relativ wenige Arbeiten die Beziehung zwischen den vielen Facetten der landwirtschaftlichen Intensivierung und der Biodiversität. Zweitens, die meisten Studien hinsichtlich Landnutzung und Biodiversität haben die Auswirkungen auf lokaler bis regionaler Skala analysiert, wohingegen nur wenige diese Beziehung auf globaler Skala untersucht haben. Diese Lücke ist besonders kritisch in Bezug auf die Vorhersage des Artenreichtums – wobei traditionellerweise eher Umweltfaktoren als durch den Menschen bedingte Faktoren als wichtig für das Bedingen und Vorhersagen von großflächigen Mustern der Biodiversität angesehen werden. Drittens, angesichts des zunehmenden zukünftigen Bedarfes an Ressourcen ist ein besseres Verständnis bezüglich der Auswirkung der zukünftigen landwirtschaftlichen Landnutzung auf die Biodiversität nötig. Diese Dissertation erzielte Fortschritte darin Brücken über diese Forschungslücken zu schlagen durch (i) das Kartieren von Mustern vielfacher Metriken der Landnutzungsintensität und Biodiversität, (ii) das Verbessern der Arten-Areal-Beziehung durch die Einbindung von Landbedeckung und Landnutzungsintensitätsmetriken sowie (iii) das Identifizieren von Gebieten mit großer biologischer Vielfalt, die gefährdet sind hinsichtlich der Trajektorien potentieller zukünftiger Landnutzungsexpansion und –intensivierung. Die Muster der Landnutzungsintensitätsmetriken waren heterogen verteilt in Gebieten mit hoher Biodiversität, was darauf hinweist, dass die Umweltschutzforschung vielfache Intensitätsmetriken einbeziehen sollte um zu verhindern, dass die Bedrohung für die Biodiversität unterschätzt wird. Weitere Ergebnisse zeigen, dass in der Vorhersage des globalen Artenreichtums die Landnutzungsintensität den Biomen in nichts nachsteht, wodurch eines der fundamentalsten Gesetze in der Ökologie erweitert wird und ein verbessertes Verständnis der großflächigen Muster im Artenreichtum erzielt wird. Die am stärksten gefährdeten Gebiete bezüglich des potentiellen zukünftigen landwirtschaftlichen Wandels wurden schließlich weitverbreitet in

Lateinamerika und im subsaharischen Afrika gefunden. Dieses Ergebnis bot wichtige Erkenntnisse zur proaktiven Entschärfung von zukünftigen potentiellen Konflikten in der Beziehung zwischen Biodiversität und Landnutzung. In Anbetracht der großen Bedrohung, die die Landwirtschaft für die Biodiversität darstellt, hob diese Dissertation insgesamt die Komplexität und Bedeutung der Landnutzungsintensität in ihrer Beziehung zur Biodiversität hervor und identifizierte Gebiete mit hoher Biodiversität, welche bedroht sind von landwirtschaftlicher Landnutzung, sowohl in der Gegenwart als auch zukünftig.





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# **Chapter I: Introduction**

## 1 Scientific background

### 1.1 Life on earth and how we shape it

Our planet's most exceptional attribute is the presence of life and the most outstanding feature of this life is its diversity. From sharks that live in underwater volcanos (Phillips, 2016), to tardigrades that can survive in space (Jönsson *et al.*, 2008), there are estimated to be approximately 8.7 million eukaryotic species on Earth. Of these, only around 14% of terrestrial species have been scientifically described (Mora *et al.*, 2011). Alongside this diversity live over 7 billion humans. Our impact on the planet and its life forms is alarming (Sanderson *et al.*, 2002). If we scale the history of Earth to the timeframe of one single year: *Homo sapiens* arrived less than twelve minutes ago, agriculture took off just over a minute ago, and the dawn of the industrial revolution began a mere two seconds ago (Bostrom, 2009). In these past few seconds, we have: reached CO<sup>2</sup> levels higher than they have been since recordings began (Mauna Loa, 400ppm, (Showstack, 2013), acidified our oceans at unprecedented rates (Orr *et al.*, 2005), and lost up to half of the world's trees (Crowther *et al.*, 2015). Currently, we appropriate 25% of global annual net primary productivity (Krausmann *et al.*, 2013) and use 54% of freshwater run-off (Postel *et al.*, 1996). In the short time-span of the past 50 years, our impact has escalated and transformed the natural world more rapidly and profoundly than ever before in history (Steffen *et al.*, 2015), likely heralding a new geological epoch: that of the Anthropocene (Crutzen, 2002).

This era of rapid global change is very likely the beginning of the sixth mass extinction on Earth (Barnosky *et al.*, 2011; Ceballos *et al.*, 2015). Humanity's collective actions are obliterating entire species at rates at least 100 times greater than the background norm (Ceballos *et al.*, 2015). Additionally, the size of wildlife populations is in rapid decline (WWF, 2014). Since 1970, in less than two human generations, while our species population size has doubled, vertebrate populations have dropped by half, with the most dramatic declines in the highly diverse neotropics (83% decline, WWF, 2014). At its root, this widespread environmental destruction and associated biodiversity loss is a result of a combination of human population growth and increased per capita consumption (WWF, 2014). Both of these drivers are central obstacles to the long-term survival of other species, but are difficult to curb.

Regarding human population growth, despite effective yet relatively small-scale interventions related to education, free access to family planning, and women's rights

(Bongaarts & Sinding, 2011; Lutz & KC, 2011), due to the momentum of the current human population size, there will likely be more than 9 billion people by the end of the century (Bradshaw & Brook, 2014; Gerland *et al.*, 2014). In conjunction with this, increased consumption of resources, including food, fibre, and bioenergy is also rising, and set to escalate as nations move out of poverty and gain an appetite for what the developed world has enjoyed for decades (Tilman *et al.*, 2011). Due mainly to an inefficient conversion ratio of grain to meat, a diet heavy in animal produce is particularly heavy in resource use (Machovina *et al.*, 2015). For example, in the US, it takes up to 25kg of grain to produce 1kg of beef, pig meat requires a grain to meat ratio of 9:1, and chickens 3:1 (Smil, 2013). Demand for meat and dairy is difficult to curb, with studies showing that while consumers do care about the environmental effect of products, when compared with the importance placed on other factors, such as price, taste, and quality, sustainability ranks last in decision making (DEFRA, 2014).

The combination of the overall number of people plus the overconsumption of resources brings us from the root to the direct drivers of biodiversity loss. The single biggest direct threat to biodiversity is agricultural activity in the form of cropping (Figure I-1), threatening over half of all known near-threatened or threatened species (Maxwell *et al.*, 2016). Agriculture is also the number one cause of tropical deforestation (Geist & Lambin, 2002) and accounts for 92 per cent of the global water footprint (WWF, 2014). Agricultural activities contribute to many other factors that threaten biodiversity including pollution, logging, land degradation, climate change, introduction of invasive species, and also the direct loss of carnivores and herbivores (Steinfeld *et al.*, 2006; Machovina *et al.*, 2015; Maxwell *et al.*, 2016).

Many species are threatened by more than one factor, and many factors themselves overlap. For example, one-third of crops are used as livestock feed (Foley *et al.*, 2011; Alexandratos & Bruinsma, 2012). Livestock, including pasture and associated cropland accounts for over half of human-appropriated biomass (Krausmann *et al.*, 2008) and three-quarters of all agricultural land, making it the single largest land use (Steinfeld *et al.*, 2006). Indeed, meat and dairy has such a huge effect on the amount of land under use, that an entirely vegan human population in 2050, would require less cropland than what was used in the year 2000, with the potential to “reforest” an area approximately the size of the entire Amazon rainforest (Erb *et al.*, 2016a).

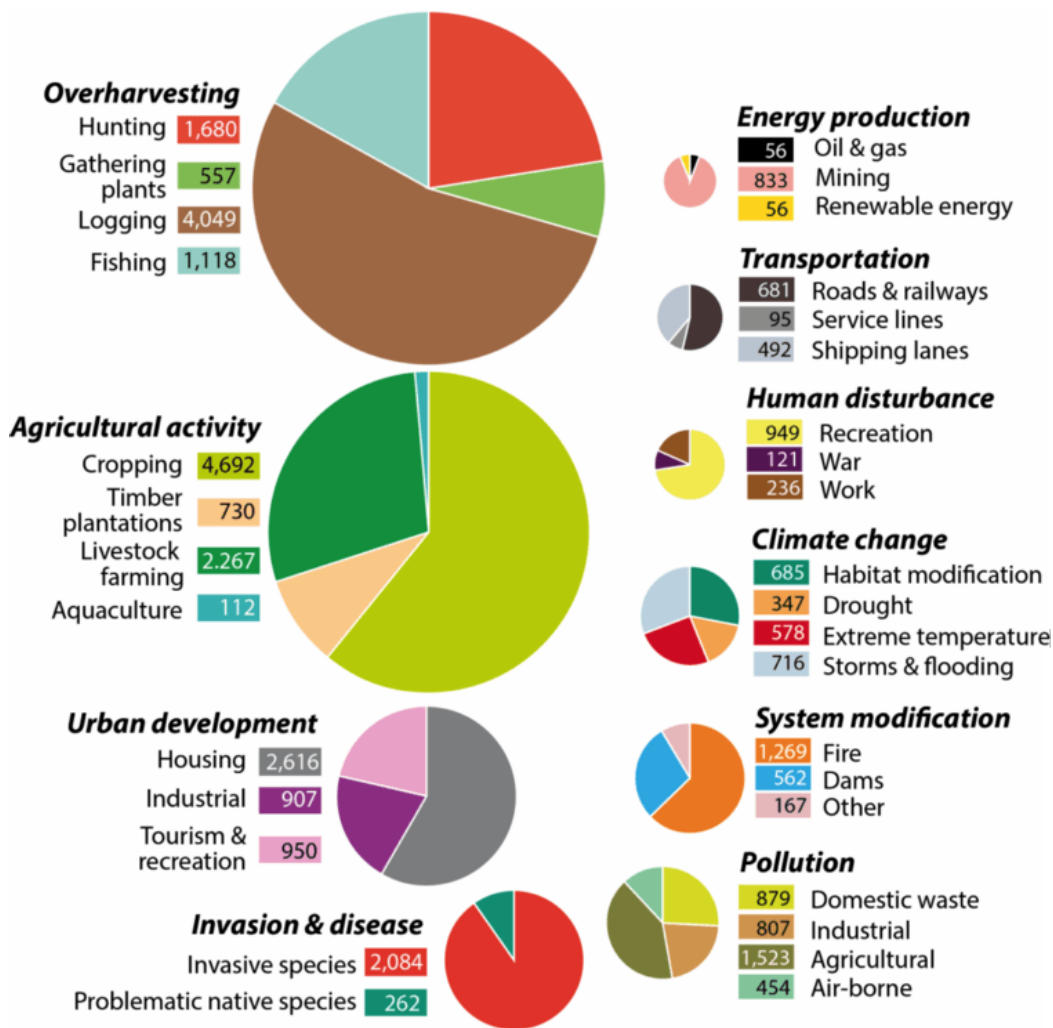


Figure I-1: The biggest threats to the world's wildlife: 62% of IUCN Red List species (5,407 species) are threatened by agriculture – over three times the number of those threatened by climate change (19%). Source: Maxwell *et al.* (2016).

Biodiversity loss is concerning for two fundamentally different but complimentary reasons. First, there is the intrinsic and essentially immeasurable value of biodiversity. This includes millions of years of evolution, the resulting diversity of life, the ethical implications of species extinction, not to mention the cultural, aesthetic, and spiritual value of the natural world and the species within (Vilka, 1997). Second, there is the instrumental value of biodiversity. Our short-term well-being and long-term ability to survive is utterly reliant on the proper functioning of natural systems, and this functioning depends on biodiversity (Hooper *et al.*, 2005). For example, biodiversity loss affects both ecosystem services and their ability to function, especially with regard to the capacity of socio-ecological systems to cope with extreme events (MA, 2005a; TEEB, 2009). In addition, the loss of a single species can trigger cascade effects and complex interactions throughout an ecosystem (Ripple *et al.*, 2014; Pérez-Méndez *et al.*, 2016). Our well-being is also reliant on medical

advances and infectious disease control, where biodiversity has been shown to play a central role in both reducing the prevalence of infectious disease (Keesing *et al.*, 2010) and providing a vast genetic storehouse for biotechnology including medicine, with over half of the top 150 prescription drugs in the United States derived from biological diversity (Grifo & Rosenthal, 1997).

Despite this, ecosystems and their functionality have been irreversibly altered (Steffen *et al.*, 2007). What is more, many thresholds that are proposed “safe” planetary boundaries have been crossed: notably biodiversity loss, the nitrogen cycle and climate change (Figure I-2; Rockstrom *et al.*, 2009). Crossing any of these boundaries could generate sudden and irreversible environmental change. Due to the biodiversity loss associated with land use, an estimated 65% of the terrestrial surface has now crossed the biodiversity loss boundary - directly threatening our well-being (Newbold *et al.*, 2016). Many uncertainties remain inherent in complex ecological systems including complex time lag effects, therefore, we are only beginning to fully comprehend the full spectrum of consequences related to biodiversity decline (Doak *et al.*, 2008; Kuussaari *et al.*, 2009).

Undeniably, biodiversity loss is one of the most critical environmental concerns of our time. In an attempt to abate this loss, the relatively young field of conservation biology was born. At its inception in the 70s and 80s, conservation was focused on establishing protected areas and keeping ‘humans out’ in order to let nature thrive (Mace, 2014). The field has since developed to include a wide variety of approaches in understanding and reducing the impact of human activities on biodiversity, including both on farm and off (Adams, 2004; Mace, 2014).

The first step in abating biodiversity loss is accurately measuring it. A commonly used approach compares current extinction rates with background rates. Research in this domain has shown species extinctions are currently between 100 and 1000 times higher than the background rate (Pimm *et al.*, 1995; Barnosky *et al.*, 2011; Ceballos *et al.*, 2015). However, this technique is broad by nature, and does not explicitly assess the causes of biodiversity loss.

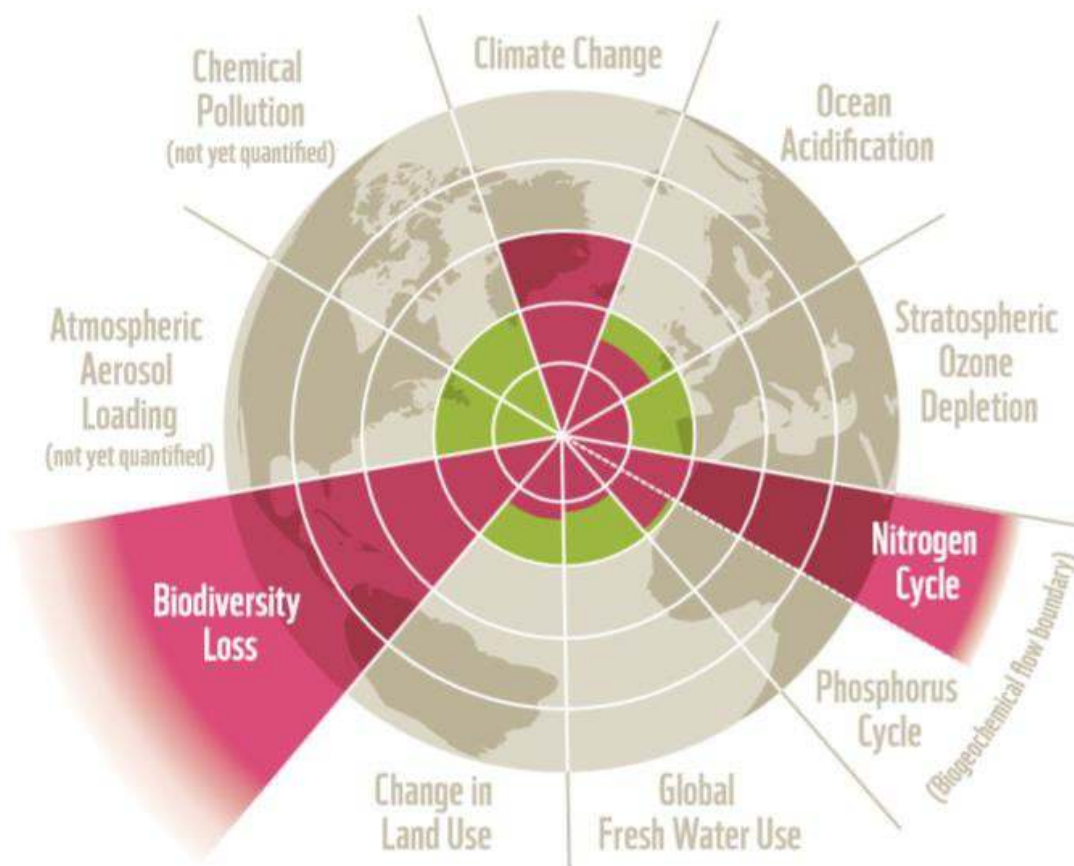


Figure I-2: Planetary boundaries - The inner green circle indicates the proposed safe operating space for nine planetary systems. The red wedges give an estimate of the current position for each planetary system. The rate of biodiversity loss, climate change and human interference with the nitrogen cycle boundaries have already been exceeded. Source: Rockstrom *et al.* (2009)

Species-area relationships (SARs) provide a step forward by relating the size of an area to the number of species found within. SARs are among the most studied relationships in ecology and are crucial to our understanding of species distributions and biodiversity dynamics (Rosenzweig, 1995; Turner & Tjørve, 2005; Drakare *et al.*, 2006; Dengler, 2009). Originally, non-natural land was thought to be inhospitable to species (Pimm *et al.*, 1995; Brooks *et al.*, 2002; Thomas *et al.*, 2004). In recent years, the ability for species to survive on and around agricultural land is being taken into account. For example, Koh and Ghazoul (2010) have developed a matrix-calibrated species-area model for predicting biodiversity loss due to land use change, and Gerstner *et al.* (2014) have improved the predictive ability of SARs in terms of plant species richness by including biomes and land-cover. However, our knowledge remains limited. Numerous factors related to species and area may affect this relationship and, if left unexamined, may miscalculate both patterns of species richness and even extinction risk (Turner & Tjørve, 2005; He & Hubbell, 2011). For example,



improvements may be possible by incorporating a wider spectrum of metrics in order to better represent the complexity of agricultural land use, rather than land-cover, which represents agricultural land in a binary present / not present form. Furthermore, the importance of human influence on species richness is often embraced at local grains (Dornelas *et al.*, 2014; Newbold *et al.*, 2015) rather than at global scales. This could be an important research gap as recent studies indicate that broader patterns of species richness, at least in terms of range size and extinction risk, might be related to human activities more than we suspect (Murray & Dickman, 2000; Di Marco & Santini, 2015). In the face of rapid biodiversity loss, there is an urgent need to develop improved approaches that may allow for better predictions of global scale SARs by including a more nuanced view of the many dimensions and pathways of agricultural activity.

## **1.2 Agricultural Pathways: expansion and intensification**

From the early development of civilizations, to present day, agricultural land use has played a crucial role not just in biodiversity loss, but also in the growth and progress of human society (MA, 2005a). Generally, there are two main pathways of increasing agricultural production in order to satisfy an increasing demand for resources: *expansion* of land-based production systems into natural areas and *intensification* of pre-existing production systems (Tilman *et al.*, 2011).

Humans began modifying the Earth's surface, to a degree that is detectable by archaeological, paleo-ecological, and environmental historical techniques, since at least the late Pleistocene (Kirch, 2005; Ellis *et al.*, 2013). This modification not only took the form of hunting and foraging, but also, around this time, large-scale land clearing and widespread agriculture is likely to have taken hold (Ellis *et al.*, 2013). Between 3,000 B.C. and 1,500 A.D. (depending on the model employed), many regions of Europe and Asia were likely under significant use (Ellis *et al.*, 2013). Historically, the most substantial changes in land use were related to agricultural expansion (Ramankutty & Foley, 1999). Land use has rapidly spread across the globe in the past three centuries, with a 466% increase in agricultural land from 1700 to 1980 (Meyer & Turner, 1992). This loss of natural habitat has previously been mostly at the expense of temperate and Mediterranean forests and woodland (Figure I-3). In the past half century, conversions have moved into tropical forest and savannas, as non-converted land in the temperate zones was already mostly exploited (Figure I-3; MA, 2005b).

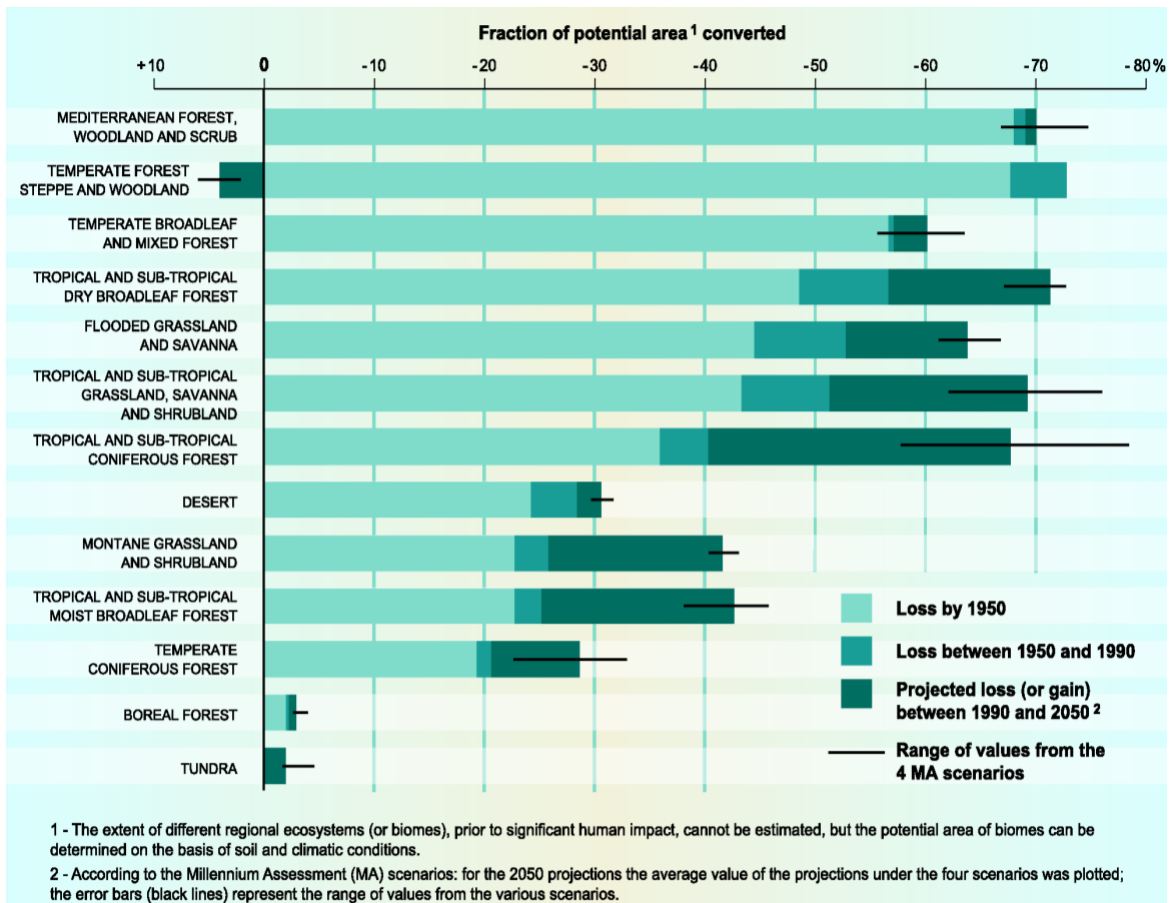


Figure I-3: Global percent conversion of ecosystems. Source: MA (2005b)

Currently, more than 38% of the world's terrestrial surface is comprised of human-dominated croplands and pastures (Ramankutty *et al.*, 2008). When excluding ice-covered land, the global proportion of land altered by human land use rises to more than 75%, with less than a quarter remaining as wildlands (Ellis & Ramankutty, 2008). In the next 40 years, it is estimated that agricultural expansion could envelope an additional 200-300 million ha of wilderness (Chaplin-Kramer *et al.*, 2015), mostly in the biodiversity rich regions of the tropics and savannas.

However, further expansion into remaining natural land is bearing increasingly high environmental and socio-economic costs (Garnett *et al.*, 2013), especially as available land for agricultural expansion is becoming scarce (Lambin & Meyfroidt, 2011). As a result, in order to meet growing demand, production increases via land-use intensification are essential (Tilman *et al.*, 2011; Mueller *et al.*, 2012).

Land-use intensity was first brought to the forefront by Malthus (1798) who predicted that the human population would be limited by inelastic and linear increases in agricultural production. Boserup (1965), on the other hand, argued that agricultural intensification and

technological innovation were a direct response to the increasing pressure of demand. So far, the Malthusian view has been proven wrong (Stokstad, 2005), with yield increases outpacing even human population growth (Matson *et al.*, 1997). Such production increases generally occur as a result of a combination of technological advances and additional inputs in terms of labour, energy, fertiliser, pesticide, and water (Matson *et al.*, 1997).

Over the past century, many large advances have been made in this respect, with the development of high-yielding seed varieties, chemical fertilisers and agro-chemicals, along with new methods of cultivation and increased irrigation infrastructure and mechanisation. All of these advances in a relatively short time earned this period the title of the 'green revolution' (Borlaug, 2007).

While most historical production increases came thanks to agricultural expansion, since the mid-20<sup>th</sup> century, global cropland production has more than doubled whilst overall maintaining approximately the same cropland area (Borlaug, 2007; Rounsevell *et al.*, 2012). In terms of feeding a growing world, land-use intensification is now one of the most dominant forces to be reckoned with (Foley *et al.*, 2011; Tilman *et al.*, 2011).

However, despite its importance, land-use intensity has not garnered the same level of research attention as agricultural expansion (Erb, 2012). This may be partly because land-use intensity is a complex and multidimensional term that is not readily measured in one metric, with no universally agreed upon definition (Erb *et al.*, 2013; Kuemmerle *et al.*, 2013). The classification scheme of Kuemmerle *et al.* (2013) and Erb *et al.* (2013) provides a step forward by splitting land-use intensity into three categories related to inputs, outputs, and system metrics. Input metrics refer to the intensity of land use along different input dimensions, such as labour, mechanisation, fertilizer and irrigation. Output metrics relate to the ratio of outputs from agricultural production and inputs, for example yields (harvests/land). System-level metrics describe the relationship between the inputs or outputs of land-based production to the overall system, for example yield gaps (actual vs. attainable yield) or the percentage of net primary production that humans appropriate (HANPP, Haberl *et al.*, 2007). This classification scheme helps to detangle the complexities inherent in land use-intensity (Kuemmerle *et al.*, 2013), and provides a required framework both for clearer measurements of land-use intensity, and for assessing its concordance with and potential impact on biodiversity.

### **1.3 The impact of agricultural expansion and intensification on biodiversity**

The main processes of agricultural production are also the main modes by which biodiversity is impacted. Expansion threatens biodiversity primarily through the destruction and fragmentation of natural habitats (Foley *et al.*, 2005; Chapin *et al.*, 2008). A range of studies have empirically demonstrated that habitat loss and fragmentation is a major cause of biodiversity loss for virtually all terrestrial taxonomic groups (Fischer & Lindenmayer, 2007). Many insect groups have been found to be highly susceptible to forest loss and fragmentation in terms of species richness and abundance (Didham *et al.*, 1996; Koh & Wilcove, 2008). Habitat loss is considered as one of the main drivers of reptile and amphibian decline, particularly in the neotropics (Alford & Richards, 1999; Stuart *et al.*, 2004). Similarly, an increase in threatened bird species has been associated with habitat destruction in many regions (Kerr & Cihlar, 2004; Koh & Wilcove, 2008). Mammals have also been found to be severely threatened by habitat loss, from near complete extinctions in small mammals in forest fragments (Gibson *et al.*, 2013) to severe range contractions and large declines in large carnivores across the globe (Ripple *et al.*, 2014). Across taxonomic groups, threats have been found to be disproportionately high for higher trophic levels (Didham *et al.*, 1996; Krauss *et al.*, 2010), where the proportion of remaining suitable habitat can be crucial in conserving species (Andren, 1994). The spatial configuration of habitat loss at the landscape scale has also been identified as an important component (Seppelt *et al.*, 2016), where more complex configurations are likely to support higher abundances of species than homogenous landscapes (Stein *et al.*, 2014).

Since expansion can often signify the destruction of remaining natural habitat that support high levels of biodiversity, there is growing support for the intensification of currently used land (Foley *et al.*, 2011; Tilman *et al.*, 2011; Mueller *et al.*, 2012). Conventional intensive management is characterised by highly mechanised, large-scale monoculture plots where high levels of agrichemicals are applied (Hudson *et al.*, 2014). The majority of these techniques are detrimental to the long-term health of the environment (Newbold *et al.*, 2015). Different intensification processes can vary substantially across the globe, as do their effects on biodiversity (Foley *et al.*, 2005; Chapin *et al.*, 2008). High inputs such as fertilisers, pesticides and irrigation can increase the risk of soil erosion, degradation (Foucher *et al.*, 2014) and salinization (Foresight, 2011). These processes can in turn reduce soil organic matter, disturb soil biota communities (Foucher *et al.*, 2014), become toxic to plants with cascading effects on ecosystems (Yamaguchi & Blumwald, 2005) and overall pose a substantial threat to birds, mammals and amphibians (Kerr &

Cihlar, 2004; Gibbs *et al.*, 2009; Kleijn *et al.*, 2009; Hof *et al.*, 2011). Intensive livestock grazing results in the removal of biomass, trampling and destruction of root systems, defecation, and replacement of wild grazers (Reid *et al.*, 2009) and can have detrimental effects on biodiversity in terms of mean species abundance and species richness (Alkemade *et al.*, 2012; Newbold *et al.*, 2015), especially when pastures lack remaining native vegetation (Felton *et al.*, 2010). Intensification processes that negatively impact biodiversity can also endure a backlash effect, where the role of biodiversity in ecosystem functioning, crop production, pest control, and resilience against invasive species is diminished (Donald, 2004; Tschardtke *et al.*, 2005). On the other hand, not all intensely managed land is necessarily detrimental to biodiversity. In contrast to the generally negative effect of industrialised farming practises, small-scale agro-ecological production techniques, which often use less agro-chemical inputs, have been found to be less destructive to biodiversity and have competitive yields (when including multi-cropping) on a per area basis (Perfecto *et al.*, 2007; Perfecto & Vandermeer, 2010; Clough *et al.*, 2011).

Despite the importance and complexity of land-use intensity's effect on biodiversity, agricultural expansion has generally garnered more research attention than intensification in estimating biodiversity loss (Pereira *et al.*, 2010) and choosing priority regions for conservation (Mittermeier *et al.*, 2004). In particular, the specifics of the relationship between global patterns of land-use intensity and biodiversity remains largely unknown. This is unfortunate considering the potential of land-use intensification in closing yield gaps and thus increasing production to meet growing demands. Yet, identifying the intricacies of this relationship is not an easy task. Even though recent advances have been made in measuring and mapping land-use intensity (Erb *et al.*, 2013; Kuemmerle *et al.*, 2013), the majority of studies investigating the impacts of land-use intensity on biodiversity have focused on a single intensity metric such as fertiliser application (Kleijn *et al.*, 2009), yields (Herzon *et al.*, 2008) or a combined index such as human pressure (Geldmann *et al.*, 2014). Moreover, as with SAR studies, most research directly assessing the impact of land use on biodiversity are local to regional in scale (Kleijn & Sutherland, 2003; Green *et al.*, 2005), with relatively few attempts to assess global relationships. These are potentially strong limitations given the multidimensionality of land-use intensity (Kuemmerle *et al.*, 2013), where each measure of land-use intensity is likely to have a different global spatial pattern and potential effect on biodiversity. Thus, when investigating the relationship between agricultural land use and biodiversity, a wider spectrum of land-use intensity metrics, at a broader scale, is lacking.

#### **1.4 Balancing agricultural production and biodiversity**

Considering the current impact of agricultural production on the world's wildlife, along with high future demand for resources, the need to balance food and fauna has never been greater (Godfray & Garnett, 2014). Arguably, the main levers in balancing agricultural production and biodiversity lie in tackling the underlying drivers of demand. These include finding ways to transform unsustainable consumption habits, providing widespread easily accessible education and family planning in order combat the rising number of consumers, and reducing food waste on every level from farm to fridge (Bongaarts & Sinding, 2011; Lutz & KC, 2011; Garnett *et al.*, 2013; Tilman & Clark, 2014). It is also worth noting here that improving small-holder land rights, food availability, access, and utility in the developing world is crucial in terms of food security – a topic that is more complex and political than simply increasing agricultural production (Barrett, 2010). Despite all of this, even under ambitious future scenarios of reducing food waste, consumption of meat and dairy, and inequality, agricultural production increases will likely still be necessary (Visconti *et al.*, 2015).

In terms of increasing production and conserving biodiversity, this balancing act has been framed by many conservation biologists as a choice between land sharing, in the form of lower yielding, wildlife friendly farming, and land sparing, by maximising production in one area in order to 'spare' or conserve another (Green *et al.*, 2005). Much research effort and heated debate has arisen from this framework (Green *et al.*, 2005; Phalan *et al.*, 2011; Phalan *et al.*, 2014). However, the land-sparing/land-sharing approach is based on a false dichotomy where one strategy must be favoured over another, whereas in reality, these approaches are by no means mutually exclusive, where a framework comprised of context specific solutions including both protected areas and wildlife-friendly farming is possible (Kremen, 2015). Furthermore, the assumptions of the land-sparing/land-sharing framework often break down when scrutinised: maximising yields in a land sparing context is no guarantee of an increase in the amount of land 'spared' for nature (Perfecto & Vandermeer, 2010; Tschardt *et al.*, 2012), especially when strict land-use planning is lacking and the demand for resources is not fixed – which is the case for meat and luxury products (Lambin & Meyfroidt, 2011). The higher efficiencies associated with agricultural intensification that can potentially spare land for nature, can also lead to lower food prices and thus higher rates of consumption (Lambin & Meyfroidt, 2011). This, in turn, can incentivise expansion. This process, known as Jevons paradox (Jevons, 1866), has been shown in many regions including Brazil, Indonesia and is likely to occur in many others, such as Sub-Saharan Africa (Angelsen & Kaimowitz, 2001; Nepstad & Stickler, 2008; Hertel *et al.*, 2014). In addition to this, land sharing or wildlife

friendly approaches, rather than having lower yields as assumed in the land-sparing/land-sharing framework (Green *et al.*, 2005; Phalan *et al.*, 2011; Phalan *et al.*, 2014), have been shown to be competitive in terms of production, especially when small-scale agro-ecological approaches are effectively employed (Cornia, 1985; Perfecto & Vandermeer, 2010).

In light of this, some side-step the beleaguered land-sparing/land-sharing debate and argue instead for ‘sustainable intensification’. However, just as ‘intensification’ is not a straightforward concept in terms of definition or measurement, sustainable intensification is more difficult still. Since ‘sustainable development’ was brought to the forefront by the Brundtland Commission (1987), hundreds of definitions of ‘sustainability’ and ‘sustainable intensification’ have been put forward with, as yet, no common understanding of the term, let alone an agreed upon definition (Petersen & Snapp, 2015).

Early discussions of ‘sustainable intensification’ were galvanised by Pretty (1997) who prioritised increasing yields while simultaneously improving both environmental and socio-economic conditions where “local knowledge and adaptive methods are stressed rather than comprehensive packages of externally-supplied technologies”. This approach favours agroecological methods that have been shown to improve yields, support local knowledge and increase food-security, whilst maintaining biodiversity (Perfecto & Vandermeer, 2010; Chappell & LaValle, 2011; Murgueitio *et al.*, 2011; Tschamtkke *et al.*, 2012). However, more recent rhetoric on ‘sustainable intensification’ has turned towards focusing on closing yield gaps by capital and input intensive means, including precision agriculture, improved nitrogen efficiency, and better access to irrigation (Foley *et al.*, 2011; Mueller *et al.*, 2012). In terms of conservation, this reframing of sustainable intensification may do more harm than good, as outlined in the previous section; such additional inputs can have many negative consequences for biodiversity.

Aside from the hazy definitions and various approaches towards ‘sustainable intensification’, many species are sensitive to habitat alteration and simply cannot survive in agricultural matrices – protected areas, to some extent, will always be needed (Kleijn *et al.*, 2011). In saying this, only 15% of the Earth’s land surface area is protected (Geldmann *et al.*, 2015), compared to more than 38% under agricultural management (Ramankutty *et al.*, 2008). Thus, many wide-ranging species, for example, endangered large carnivores, cannot persist in small pockets of protected areas, but need a larger connected matrix of semi-natural and natural areas (Ray *et al.*, 2013b).

The land-sparing/land-sharing framework was useful in bringing the issue of food and fauna to the table. Alongside this, the concept of sustainable intensification, particularly in the form of agro-ecological approaches, holds great promise but are currently practiced on a relatively small- scale (Altieri, 2004). In light of rising demand for resources, and considering the main modes of agricultural development that are likely to be employed to meet such demand, there is also an urgent and less publicised need to look towards how and where the main modes of agriculture may threaten biodiversity, both currently and in the future. Despite the fact that agriculture threatens over three times more species than climate change (Maxwell *et al.*, 2016), most studies assessing future biodiversity loss focus on the impact of climate change (Titeux *et al.*, 2016). Of the relatively few studies that have explored what future land-use change may mean for biodiversity (Titeux *et al.*, 2016), most do so within the framework of integrated assessment models (IAMs; Sala *et al.*, 2000; Visconti *et al.*, 2011; de Baan *et al.*, 2013; Bellard *et al.*, 2014; Rondinini & Visconti, 2015; Visconti *et al.*, 2015). However, such complex models cannot take into account the unpredictable and extreme nature of shock events (Müller *et al.*, 2014; Jepsen *et al.*, 2015; Ramankutty & Coomes, 2016). Thus, an overview of areas most at risk under the main modes of future agricultural change, in terms of the biophysical option space of potential agricultural intensification and expansion is urgently needed.

## **2 Conceptual framework**

### **2.1 Research questions and objectives**

*The overarching goal of this thesis is to advance scientific understanding of the relationship between agricultural land use and biodiversity.* To achieve this goal, this thesis is subdivided into three main sections related to three core research questions.

*Research Question I: How do patterns of land-use intensity relate to patterns of biodiversity?*

Land-use intensification is often touted as a solution to curtail expansion into natural areas and grow more on the same patch (Green *et al.*, 2005; Phalan *et al.*, 2011; Tilman *et al.*, 2011). However, conservation research has generally focused on expansion rather than intensification (Mittermeier *et al.*, 2004; Pereira *et al.*, 2010). Where intensification has been included, most research focuses on single metrics of land-use intensity, primarily yield gaps (Green *et al.*, 2005; Phalan *et al.*, 2011). A more in-depth view of patterns of land-use intensity and biodiversity requires appropriate global scale datasets. Up until recently, such datasets, particularly with regard to land-use intensity, were not available. However, thanks



to recent advances in remote sensing image analysis and approaches that combine such images with ground-based inventories, along with updated expert-based biodiversity datasets, new opportunities in investigating the complex relationship between land use and biodiversity arise. In finding sustainable ways to produce food, it is essential that the full spectrum of management practises by which food is grown is taken into account.

Chapter II tackles the absence of land-use intensity's multiple facets in conservation research and addresses the first research question by compiling a geodatabase of 13 recently available land use and land-use intensity datasets in terms of input, output and system metrics, and comparing their spatial concordance with global endemism richness distributions for birds, mammals and amphibians. This approach allows for the identification of areas where biodiversity coincides with any one indicator from a spectrum of land-use intensity metrics.

The main objectives to answer *Research Question I* were to:

- (1) compile a geodatabase of global land-use intensity metrics in terms of input, output and system metrics
- (2) map the spatial patterns and hotspots of land-use intensity and biodiversity

The knowledge gap between land-use intensity and biodiversity is not just related to spatial patterns, but also to our ability to predict broad scale species richness, leading to the second research question.

*Research Question II: To what extent does the inclusion of land cover and land-use intensity improve global SAR models?*

Species-area relationships (SARs) are a crucial component of our understanding of patterns of species richness. However, two key issues remain: first, agricultural land use is the leading driver of biodiversity loss, with future land use change expected to accelerate such loss (Sala *et al.*, 2000; Newbold *et al.*, 2015), but the ability of global land-use intensity metrics to predict species richness has not been previously tested. Second, at local grains the importance of human influence on species richness is often embraced (Dornelas *et al.*, 2014; Newbold *et al.*, 2015), however, global scale studies generally focus on natural biophysical factors and fail to consider the human drivers that may be at play (Hawkins *et al.*, 2003b; Hawkins *et al.*, 2003a; Field *et al.*, 2009; Hortal *et al.*, 2012). Figuring out whether human related indicators are relevant at a global scale could add to our understanding of one of the most fundamental concepts in ecological research and may allow for better predictions of large-scale patterns of species richness.

Chapter III employs the geodatabase brought together in Chapter II in order to test whether SARs vary across regions of different agricultural land cover and a range of land-use intensity indicators representing input metrics (e.g. fertilizer, irrigation), output metrics (e.g. yields) and system-level metrics of intensity (e.g. HANPP). The resulting SARs were systematically compared in terms of their predictive ability. To do this, simultaneous autoregressive models were employed. This approach allows for spatial autocorrelation in the model residuals by including a second error term which explicitly models spatial dependence (Dormann, 2007). Overall, this method provides a better understanding of whether human based factors are relevant in predicting species richness on a global scale.

The main objective to answer *Research Question II* was to:

- (1) assess whether SARs are improved by better representing the geographic variation of its parameters in terms of land cover and land-use intensity

While an improved understanding of current biodiversity patterns is crucial, a rising demand for resources calls for more in-depth insights in how future agricultural development may influence biodiversity. This leads to the third research question.

*Research Question III: How may future pathways of agricultural expansion and intensification threaten biodiversity?*

Agricultural land use change is currently and will continue to be a leading cause of biodiversity loss (Sala *et al.*, 2000; Foley *et al.*, 2005). Only relatively few studies have investigated the relationship between potential future agricultural land use change and biodiversity loss (Titeux *et al.*, 2016). Of these, the majority of studies utilize land use projections from a small number of highly constrained development scenarios (IAMs). In a future beset with a rapidly increasing demand for natural resources, more straightforward and transparent approaches that test the biophysical option space of future agricultural pathways can serve to indicate where timely land-use planning could avert potential future biodiversity loss.

Chapter IV addresses the third research question by exploring how future conventional agricultural change may affect biodiversity. Three agricultural development pathways representing the main modes of agricultural change were created: (i) expansion into suitable land, (ii) intensification of existing cropland, and (iii) both expansion into suitable land and intensification on recently converted and long-standing cropland. This was achieved by

combining four recently available land cover and land-use intensity datasets with those used in Chapter II and III, in order to create a 1km<sup>2</sup> land-systems map with associated agricultural development pathways. How these pathways may affect local species richness and abundance was then assessed using model results from a database of over 1 million data points on the local effects on biodiversity of various types of land use and land-use intensity (Hudson *et al.*, 2014; Newbold *et al.*, 2015). High biodiversity regions at-risk of agricultural change were identified on a scale ranging from 1km<sup>2</sup> to national level.

The main objectives to answer *Research Question III* were:

- (1) develop pathways of agricultural development that represent the most common modes of land-use change
- (2) identify the most at risk regions where high biodiversity and future land-use change may coincide

In sum, a better understanding of how global patterns of agricultural land use relate to biodiversity patterns is needed. Moreover, upgrading one of the most fundamental laws in ecology, the species-area relationship, would allow for a better representation of land-use intensity and thus an improved understanding of broad-scale species richness patterns. Finally, comparing the biodiversity impact of transparent land use pathways to highlight areas most at risk under potential future change is crucial in light of rising agricultural demand.

## 2.2 Structure of this thesis

This thesis consists of five chapters: the introduction (Chapter I) is followed by three core research chapters (Chapter II-IV) that relate to the objectives and research questions described above, and a synthesis (Chapter V) that summarises results from the three preceding chapters, and provides potential applications and directions for future research. The three research chapters were written as stand-alone manuscripts, which were either published in or submitted to international peer-reviewed journals. Since each research chapter serves as an independent article, there is a limited amount of recurring material, especially in the introduction and limitation sections.

Chapter II **Kehoe, L., Kuemmerle, T., Meyer, C., Levers, C., Václavík, T., and Kreft, H.** (2015). *Global patterns of agricultural land-use intensity and vertebrate diversity. Diversity and Distributions, 21, 1308–1318.*

- Chapter III **Kehoe, L., Senf, C., Meyer, C., Gerstner, K., Kreft, H., and Kuemmerle, T.** (2016). *Agriculture rivals biomes in predicting global species richness. Ecography, in press.*
- Chapter IV **Kehoe, L., Romero-Muñoz, A., Estes, L., Kreft, H., Polaina, E., and Kuemmerle, T.** (in review). *Nature at risk: Modelling global biodiversity loss due to pathways of agricultural expansion and intensification.*





**Chapter II:**  
**Global patterns of agricultural land-use  
intensity and vertebrate diversity**

*Diversity and Distributions, 2015, Volume 21, Pages 1308–1318*

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## **Abstract**

*Aim:* Land-use change is the single biggest cause of biodiversity loss. With a rising demand for resources, understanding how and where agriculture threatens biodiversity is of increasing importance. Agricultural expansion has received much attention, but where high agricultural land-use intensity (LUI) threatens biodiversity remains unclear. We address this knowledge gap with two main research questions: (1) Where do global patterns of LUI coincide with the spatial distribution of biodiversity? (2) Where are regions of potential conflict between different aspects of high LUI and high biodiversity?

*Location:* Global

*Methods:* We overlaid thirteen LUI metrics with endemism richness, a range size-weighted species richness indicator, for mammals, birds and amphibians. We then used local indicators of spatial association to delineate statistically significant ( $p < 0.05$ ) areas of high and low LUI associated with biodiversity.

*Results:* Patterns of LUI are heterogeneously distributed in areas of high endemism richness, thus discouraging the use of a single metric to represent LUI. Many regions where high LUI and high endemism richness coincide, for example in South-America, China and Eastern Africa, are not within currently recognized biodiversity hotspots. Regions of currently low LUI and high endemism richness, found in many parts of Mesoamerica, Eastern Africa, and Southeast Asia, may be at risk as intensification accelerates.

*Main Conclusions:* We provide a global view of the geographic patterns of LUI and its concordance with endemism richness, shedding light on regions where highly intensive agriculture and unique biodiversity coincide. Past assessments of land-use impacts on biodiversity have either disregarded LUI or included a single metric to measure it. This study demonstrates that such omission can substantially underestimate biodiversity threat. A wider spectrum of relevant LUI metrics needs to be considered when balancing agricultural production and biodiversity.



## 1 Introduction

For more than 10,000 years, land use has played a crucial role in the development of human societies. Humans rely on agriculture and forestry for food, fibre, and bioenergy (MA, 2005a) and have already modified 75% of the Earth's ice-free terrestrial surface of which 12% is dedicated to cropland and 22% to pasture (Ramankutty *et al.*, 2008), with less than a quarter remaining as wildlands (Ellis & Ramankutty, 2008). This is expected to escalate further, as demand for biomass will increase drastically in the coming decades due to growing human population, surging consumption, changing diets, and demand for bioenergy (Ellis & Ramankutty, 2008; Pereira *et al.*, 2010; Smith & Zeder, 2013). Even under ambitious future scenarios of reducing food waste, consumption of meat and dairy, and inequality, production increases and related land-use change will still be necessary (Visconti *et al.*, 2015). This is problematic because land-use change is the main driver of the on-going biodiversity crisis, primarily via habitat loss and fragmentation (Sala *et al.*, 2000; Foley *et al.*, 2005) but also via the introduction of exotic species (Clavero & García-Berthou, 2005; Ellis *et al.*, 2012) and increased hunting due to access from new road construction (Laurance *et al.*, 2009). In general, biodiversity loss can have repercussions on ecosystem functioning (Tilman *et al.*, 2012), resilience of socio-ecological systems (MA, 2005a), and the welfare of human societies (MA, 2005a; TEEB, 2009). Therefore, understanding land-use effects on biodiversity is of prime importance.

Agricultural land-use change occurs in two main modes: expansion of agricultural land into uncultivated areas, or intensification of existing agricultural land. Expansion threatens biodiversity mainly through the loss and fragmentation of natural habitats (Foley *et al.*, 2005; Chapin *et al.*, 2008). Studying habitat conversion and biodiversity has therefore received much attention both in terms of quantifying biodiversity loss (Pereira *et al.*, 2010) and in choosing priority regions for conservation (Mittermeier *et al.*, 2004). On the other hand, the spatial patterns of intensification of agricultural land in concordance with biodiversity remains poorly understood.

For the purpose of our paper, we define agricultural land-use intensity as the degree of adoption of land management practices enabling yield increases from a given area of agricultural land (Matson *et al.*, 1997; Ellis *et al.*, 2013). Yields are a commonly used measure of land-use intensity (hereafter: LUI). Yet, different practices can result in yield increases. For example, increasing fertiliser, mechanization or irrigation may have different environmental outcomes. Moreover, regions with similar yields should not be considered equally intensive if these regions differ in bioclimatic conditions which can constrain

agriculture (e.g., potential yields, Neumann *et al.*, 2010). As such, LUI is a multi-dimensional issue that relates to a range of individual processes linking people and the land and therefore cannot be fully represented by only one metric (Erb *et al.*, 2013; Kuemmerle *et al.*, 2013).

Different intensification processes can vary substantially across the globe, as do their effects on biodiversity (Foley *et al.*, 2005; Chapin *et al.*, 2008). Intensive agriculture can have particularly detrimental effects on biodiversity (Benton *et al.*, 2003; Alkemade *et al.*, 2010), including negative effects on species richness (Herzon *et al.*, 2008; Flynn *et al.*, 2009), population size (Donald *et al.*, 2001) and the loss of functional diversity (Herzon *et al.*, 2008; Flynn *et al.*, 2009). Fertilisers have been shown to negatively affect biodiversity and, along with pesticides, pose a substantial threat to biodiversity for birds, mammals and amphibians (Kerr & Cihlar, 2004; Gibbs *et al.*, 2009; Kleijn *et al.*, 2009; Hof *et al.*, 2011). Irrigation causes salinization of soils which can prove toxic to plants with cascading effects on ecosystems (Yamaguchi & Blumwald, 2005), while intensive livestock grazing can have detrimental effects on biodiversity (Alkemade *et al.*, 2012) especially when pastures lack remaining native vegetation (Felton *et al.*, 2010). In contrast, small-scale agro-ecological production practices, which often use less agro-chemical inputs, have been found to be less destructive to biodiversity than industrial practices on a per area basis (Perfecto & Vandermeer, 2010).

However, the relationship between global patterns of LUI and biodiversity is largely unknown since most of the research on LUI and biodiversity is local to regional in scale (Kleijn & Sutherland, 2003; Green *et al.*, 2005) and most studies to date focus on a single LUI metric such as fertiliser application (Kleijn *et al.*, 2009), yields (Herzon *et al.*, 2008) or a combined index such as human pressure (Geldmann *et al.*, 2014). These are potentially strong limitations given the multidimensionality of LUI.

Such knowledge gaps are alarming since a large proportion of global land-use change has historically occurred along intensification gradients (Rudel *et al.*, 2009). Particularly since the 1950s, intensification has accelerated rapidly, with irrigated lands increasing twofold (FAOSTAT, 2010) and fertiliser application up to fivefold (Tilman *et al.*, 2001). As fertile land becomes scarce and environmental costs of converting natural habitat into agricultural land less acceptable, further intensification of existing agricultural land is likely. Indeed, 'sustainable intensification' pathways are gaining considerable support (Foley *et al.*, 2011; Mueller *et al.*, 2012). Since production is higher on intensified agricultural land, this could,

in theory, result in less overall pressure on natural ecosystems, i.e., a land sparing effect, leading to more land potentially set aside for conservation (Green *et al.*, 2005). However, a land sparing effect is not guaranteed and is only possible in combination with strong governance (Byerlee *et al.*, 2014).

Recent developments in framing LUI (Erb *et al.*, 2013; Kuemmerle *et al.*, 2013), high-resolution LUI datasets (see Panel SI II-1) and global biodiversity metrics (Kier *et al.*, 2009) all provide new opportunities for analysing how spatial patterns in LUI relate to biodiversity patterns. Here, we acknowledge the multifaceted nature of LUI and compare global patterns of biodiversity with a suite of thirteen agricultural LUI metrics (Panel SI II-1 & Table SI II-1), each of which represent different dimensions of LUI. As our biodiversity metric, we chose endemism richness (Kier & Barthlott, 2001) for birds, mammals and amphibians, which is an indicator of the importance of a grid cell for conservation and combines aspects of species richness and geographic range size.

We specifically addressed two main questions: (1) Where do global patterns of LUI coincide with the spatial distribution of biodiversity? (2) Where are regions of potential conflict between different aspects of high LUI and high biodiversity?

## 2 Methods

### 2.1 Data

#### *Global land-use intensity datasets*

We compared thirteen land use datasets measuring different aspects of agricultural intensity. Our datasets are from circa the year 2000 - the time period where such datasets are richest at the global scale (Table SI II-1, Kuemmerle *et al.* 2013). To group our intensity metrics, we utilised the classification scheme of Kuemmerle *et al.* (2013) where LUI metrics are split into three categories related to inputs, outputs and system metrics. Input metrics refer to the intensity of land use along different input dimensions, such as fertiliser and irrigation. Output metrics relate to the ratio of outputs from agricultural production and inputs, e.g., yields (harvests/land). System-level metrics describe the relationship between the inputs or outputs of land-based production to the overall system, e.g., yield gaps (actual vs. attainable yield).

For input metrics, we chose a cropland extent map (Panel SI II-1, Ramankutty *et al.*, 2008), which combines national and sub-national agricultural inventory data with satellite-derived land cover data and forms the basis for yields and harvested areas of 175 of the world's

major crops (see Monfreda *et al.*, 2008). For irrigated cropland, we used a dataset which accounts for areas equipped for irrigation (Panel SI II-1, Siebert *et al.*, 2005). We also used the most fine-scale nitrogen fertiliser input dataset available (kg N/ha applied to croplands, Panel SI II-1, Potter *et al.*, 2010).

For output metrics, we selected crop yields for maize, wheat and rice (Panel SI II-1, Monfreda *et al.*, 2008), since together, they represent approximately 85% of global cereal production (Hafner, 2003). Palm oil and soybean harvested areas (Panel SI II-1, Monfreda *et al.*, 2008) were also included due to their expansion in the tropics and considerable conservation concern (Gasparri *et al.*, 2013; Wilcove *et al.*, 2013). We included livestock heads per km<sup>2</sup> using the ‘Gridded Livestock of the World’ database (Panel SI II-1, Wint & Robinson, 2007).

For system-level metrics, we included yield gaps for maize, wheat, and rice (Panel SI II-1, Neumann *et al.*, 2010) and Human Appropriation of Net Primary Productivity (HANPP, Panel SI II-1, Haberl *et al.*, 2007). System metrics differ from output metrics in that they relate inputs or outputs to system properties. While system metrics thus capture the intensity of the land system as a whole, they do so at the cost of obscuring individual properties of intensification. Yield gaps here refer to the difference between the actual yield (Panel SI II-1, Monfreda *et al.*, 2008) and estimated potential yield (t/ha) calculated by integrating biophysical and land management-related factors (Panel SI II-1, Neumann *et al.*, 2010). To interpret yield gaps in the same way as our other intensity metrics, we took the inverse of yield gaps so that higher numbers (i.e., lower yield gaps) relate to higher LUI. We additionally chose HANPP, as it provides a measure of the percentage of NPP that humans extract from the land, thus providing an indicator of the impact of agricultural management on ecosystems in terms of the inputs and outputs of land-based production (Panel SI II-1, Haberl *et al.*, 2007).

### *Global biodiversity datasets*

Endemism richness for bird, mammal and amphibian diversity were created from expert-based range maps (Panel SI II-1, Birdlife, 2012; IUCN, 2012). We scaled the data to an equal area grid of 110 x 110 km (approximately 1 degree at the equator) as finer resolutions are not recommended at the global scale due to an over-estimation of species occurrences (Hurlbert & Jetz, 2007). We chose endemism richness (Kier & Barthlott, 2001; Kier *et al.*, 2009) as it combines aspects of both species richness and species’ range-sizes within an assemblage. Endemism richness was calculated as the sum of the inverse global range sizes

of all species present in a grid cell. In order to compare our results with conservation priority areas, we chose the Conservation International (CI) hotspots (Myers *et al.*, 2000; Mittermeier *et al.*, 2004) as they are the only global scheme that prioritizes regions based on high vulnerability and irreplaceability (Brooks *et al.*, 2006). Furthermore, a substantial proportion of conservation funding is directed towards CI hotspots (Brooks *et al.*, 2006).

## **2.2 Analysing the spatial patterns of land-use intensity and biodiversity**

All LUI datasets were rescaled to the 110 x 110 km resolution of the endemism richness datasets by taking the mean value for each grid cell. We overlaid the different LUI maps with endemism richness. This allowed us to explore differences in emerging patterns, depending on LUI metrics and taxonomic classes for mammals, birds and amphibians. We then delineated high pressure regions of high LUI and high endemism richness by abridging datasets to the top 2.5% of the distribution, following the hotspot definition of Ceballos and Ehrlich (2006). We used the LUI datasets to generate maps of high pressure regions by intersecting all LUI metrics with endemism richness. To differentiate the importance of individual LUI metrics in high pressure regions, we created flower charts by calculating the relative values (in percentiles) per LUI metric (Figure SI II-1 & Figure SI II-2 show the top 2.5%, 5%, & 10% hotspot maps for each metric, top 2.5% hotspot information is shown in Table SI II-2).

In order to complement the qualitative approach with statistical quantifications, we calculated the spatial associations between LUI and endemism richness using the bivariate Moran's I metric, also known as a local indicator of spatial association (LISA; Anselin, 1995). This metric indicates the spatially-explicit strength of associations between two variables and results in (1) high-high values, here, where high endemism richness is surrounded by neighbouring cells of high LUI, (2) high-low values, high endemism richness surrounded by low LUI, (3) low-high, and (4) low-low (results for all metrics are provided in Figure SI II-3). The strength of the relationship was measured at the 0.05 level of statistical significance calculated by a Monte Carlo randomization procedure based on 999 permutations (Using GeoDa 1.4 software). Associating endemism richness values with intensity metrics in the neighbouring cells is important because simple cell overlap (used to create the concordance maps) can be affected by differences in spatial resolution or noise in the data. We used the resulting statistically significant areas to generate summary maps of high and low pressure regions for all metrics (Figure II-2 and Figure SI II-4).

### 3 Results

Regarding our first research question, we found that the location and extent of regions of low LUI were similar across metrics, often representing deserts or ice-covered land. However, within agricultural lands, the spatial concordance of high LUI and high endemism richness varied substantially in space depending on the metric chosen (Figure II-1).

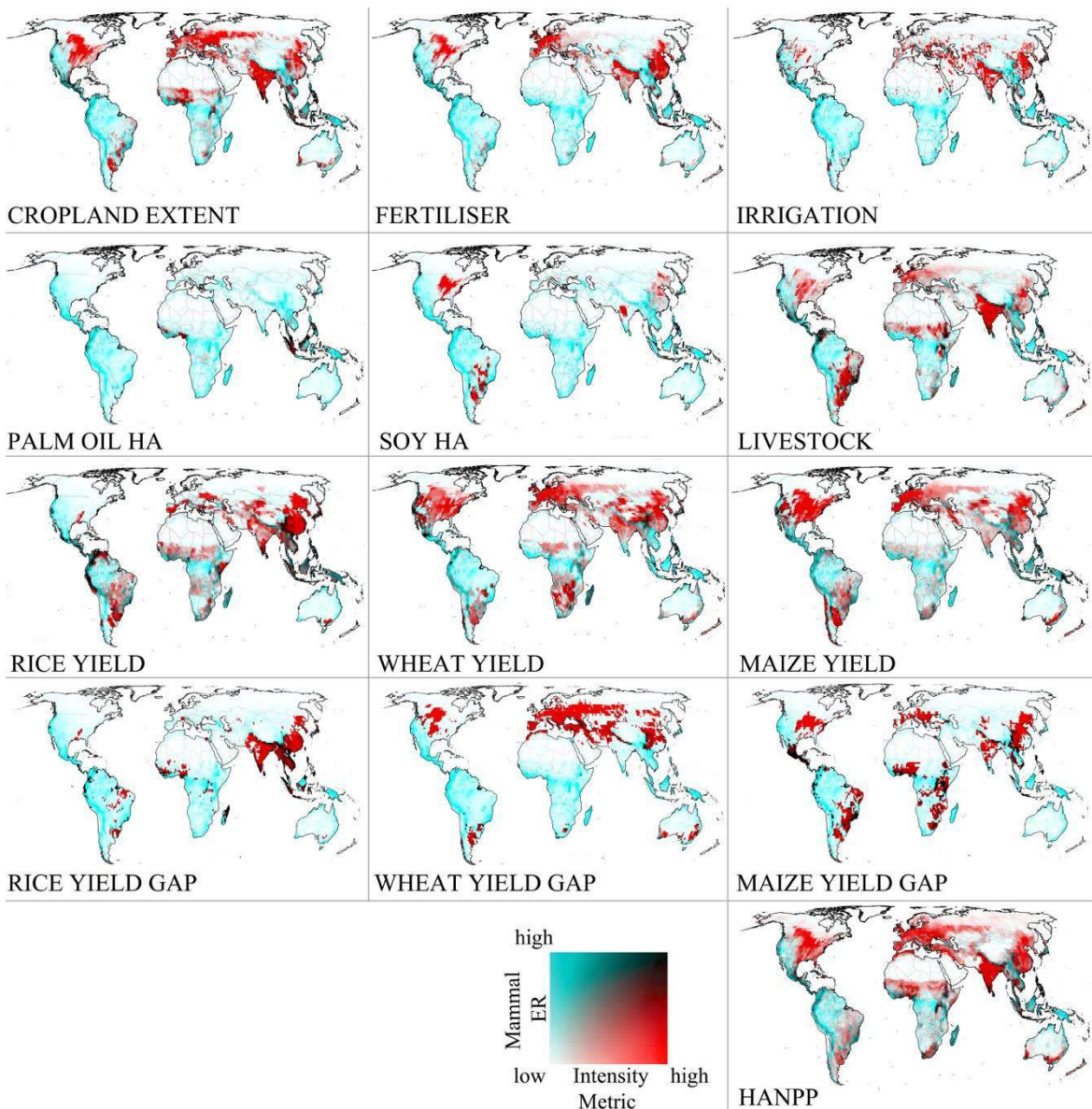


Figure II-1: Concordance maps of mammal endemism richness and land-use intensity (LUI). Note: We took the inverse of yield gaps so that higher numbers relate to higher land-use intensity. HA refers to Harvested Area. Mammal endemism richness is represented in aquamarine and LUI in red. Darker areas show where both metrics have high overlapping values, lighter areas indicate lower values (Eckert IV projection, see online article for colour version).

In relation to our second research question, regions of potential conflict between different aspects of high LUI associated with high endemism richness were found primarily in the tropics, with different combinations of high LUI metrics associated with high endemism richness. For example, for input metrics associated with high endemism richness, high fertiliser use was found in China, Southeast Asia and Europe, and irrigation was concentrated in large areas of the U.S., India, the Middle East and China (Figure II-1).

Regarding output metrics, high livestock densities were found in large regions of Latin America and India (Figure II-1). Palm oil plantations showed high concordance with endemism richness patterns, exerting substantial pressure in most areas where palm oil is grown, especially in Nigeria, the Republic of Guinea, Malaysia and Indonesia (Figure II-1). Pressure on endemism richness from high-intensity soybean cultivation was particularly high in Brazil, Argentina and Indonesia (Figure II-1). Rice yields had the highest area of overlap with endemism richness (Figure II-1). Over 50% of total land cover in the Indomalayan region and 20% of the Neotropics was found to have both high rice yields and high endemism richness (Figure SI II-5, from statistically significant local indicators of spatial association).

Finally, for system metrics, HANPP was associated with endemism richness in large areas of the tropics including Mesoamerica, southern India and Sri Lanka, and many parts of Eastern Africa and Southeast Asia. HANPP also highlighted some areas (e.g., South Africa) which were not captured by any other indicators used here (Figure II-1).

High endemism richness associated with low LUI were found in many tropical regions (Figure II-1 & Figure SI II-3). Specifically, high yield gaps due to currently low levels of irrigation and fertiliser input (Mueller *et al.*, 2012) were found in Southeast Asia, Mesoamerica and Sub-Saharan Africa. Concordance of low HANPP and high endemism richness occurred in large regions of the tropical Andes, the Amazon, Central Africa and Southeast Asia (Figure II-1 & Figure SI II-3). Conversely, our analyses showed that developed countries with an industrialized agricultural sector such as Europe and North America had particularly high LUI coupled with comparatively low endemism richness (Figure II-1 & Figure SI II-3).

When comparing between mammals, birds and amphibians, broad patterns of endemism richness were remarkably similar and highly correlated. All biodiversity metrics were found to have positive and significant spearman rank correlation coefficients ( $p < 0.05$ ) of over 0.84, including between endemism and species richness (Table SI II-3). Mammals and birds

showed exceptionally high correlations, both for endemism richness (0.95) and species richness (0.96). In terms of spatial patterns of high endemism richness congruent with LUI, relatively small differences were found between taxonomic classes. Most differences were found for amphibians, where small species ranges resulted in smaller areas associated with high LUI compared to birds and mammals (Figure SI II-6). Amphibians were the only taxon found that coincided with high yields and high HANPP in the South-eastern U.S. In the Caucasus, mammals were the only taxon present in concordance with high LUI (for all metrics, see Figure SI II-3). Birds stood out as not having any areas of high endemism richness associated with high LUI in Europe, where mammals and amphibians coincided with high LUI in areas of the Alps, the Pyrenees and parts of Italy. Birds also exhibited higher concordance with livestock in Latin America and cropland extent in South-eastern Australia than other taxonomic classes. Overall, birds and mammals showed strikingly similar spatial patterns, where ~80% of high mammal endemism richness associated with high LUI overlapped with high bird endemism richness.

When comparing between LUI metrics, the highest correlation was found between cropland extent and fertiliser use (0.92, Table SI II-3). With the exception of wheat yield gaps and palm oil harvested area, all LUI metrics had positive correlation coefficients. However, over half of the correlations between LUI metrics were below 0.5. Correlations between taxonomic classes were higher than those found between most LUI metrics. Correlations between biodiversity indicators and LUI metrics were highest for livestock density, HANPP, and maize yields.

In order to identify regions where any one LUI metric was associated with one or more taxonomic classes, we combined individual results of local indicators of spatial association (LISA) by LUI metric and taxonomic class (see Figure II-2 for combined taxa and Figure SI II-7 for mammals, birds and amphibians separately). When these results were compared with CI hotspots, we found that over half (~55%) of CI hotspots (Mittermeier *et al.*, 2004) fell within our regions of high LUI and high endemism richness. However, substantial areas of high endemism richness, for all three taxonomic classes, and high LUI were highlighted which are not currently contained within CI hotspots and include, Papua New Guinea (due to high maize and rice yields), Venezuela (high maize and rice yields and livestock density), parts of China (fertiliser, irrigation, livestock density and wheat, maize and rice yields), Eastern Africa (wheat yields and livestock density) and Eastern Australia (maize yields, HANPP and livestock density).



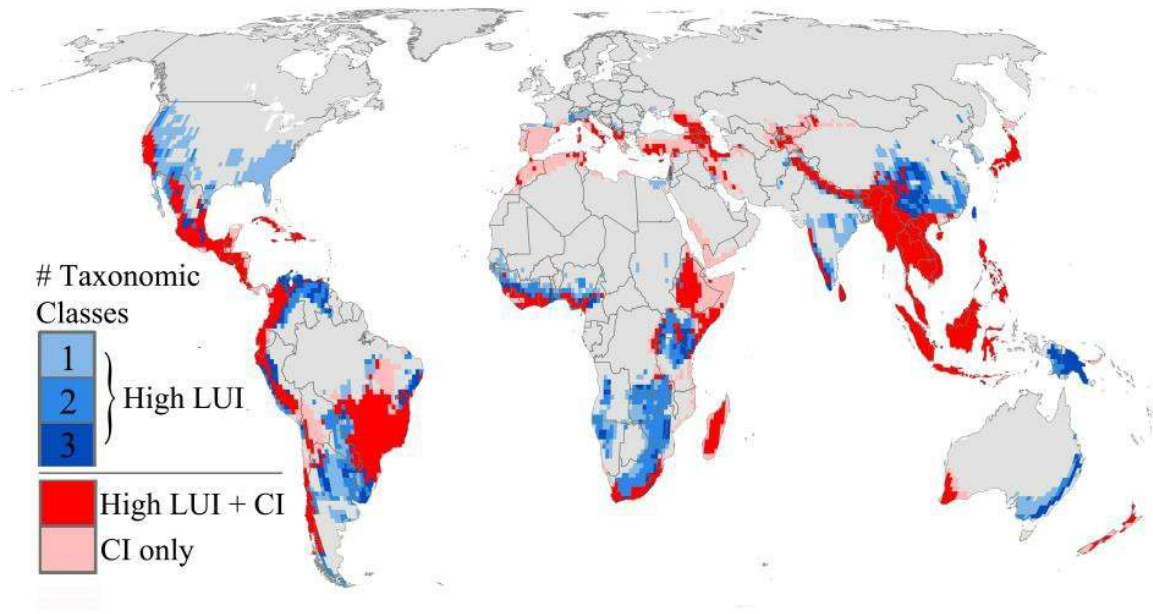


Figure II-2: Regions of high land-use intensity (LUI) and high endemism richness for mammals, birds and amphibians from statistically significant ( $p < 0.05$ ) local indicators of spatial association. Dark blue regions show high endemism richness for all three taxonomic classes associated with at least one LUI metric. Biodiversity hotspots from Conservation International (CI) which do not overlap with our high LUI & high endemism richness areas are shown in pink. Red areas signify regions of overlap between high LUI & high endemism richness (for at least one taxonomic class) and CI hotspots (Eckert IV projection, see online article for colour version).

We then investigated areas of potential conflict between high LUI and high endemism richness by overlaying the top 2.5 per cent of our metrics' geographic pattern (Figure II-3). With the exception of the Sulawesi lowlands (70th percentile rank for amphibians), all other areas exhibited relatively high bird, mammal and amphibian endemism richness, highlighting relatively small differences in spatial patterns between taxonomic classes in areas of high LUI (Table SI II-2).

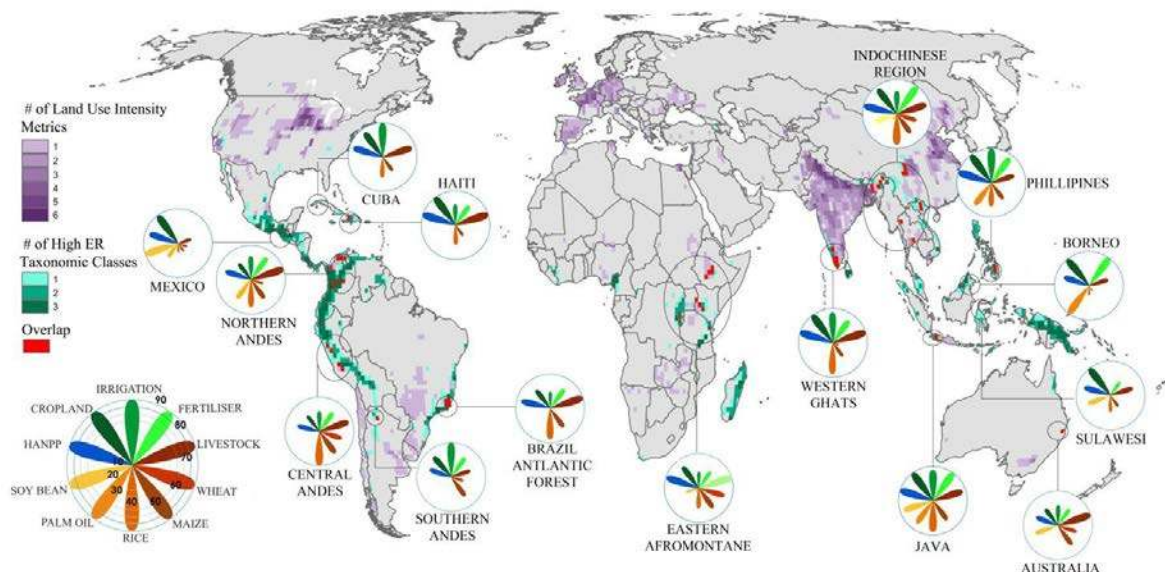


Figure II-3: Top 2.5% of land-use intensity (LUI) and endemism richness. where any one top 2.5% intensity metric overlaps with any one top 2.5% of endemism richness (ER) for mammals, birds and amphibians, thus highlighting regions of particularly high pressure between human activity and wildlife (shown in red). Multiple overlapping LUI metrics of top 2.5% are shown in purple and multiple top 2.5% of endemism richness for taxonomic classes shown in turquoise. Numbers on the petal diagram represent percentile ranks for each LUI metric. Larger petals indicate higher percentile ranks, and thus higher intensity of land use. Petals for input metrics are coloured in green, output metrics in orange and system metrics in blue. Percentile ranks for inverse yield gaps are given in Table SI II-2 (Eckert IV projection, see online article for colour version).

In contrast, peaks in the LUI metrics (top 2.5% percentile) in concordance with high endemism richness varied considerably, emphasizing large spatial differences between LUI metrics. All top 2.5% high pressure regions overlapped with CI hotspots (Australian hotspot identified by Myers *et al.*, 2000; Mittermeier *et al.*, 2004 contained all other hotspots).

#### 4 Discussion

While our results largely support previous research - that biodiversity threat is found primarily in the tropics - two main insights emerge from our work. We find that different LUI metrics resulted in diverse and incongruent spatial patterns associated with endemism richness. This emphasizes the need to move from one-dimensional approaches of representing LUI towards including multiple facets of how we manage agricultural land. We then identified regions of potential conflict between agriculture and biodiversity conservation. These regions highlight the spatial differences between LUI metrics in highly biodiverse areas with particularly intensive land use.

Diverse global intensity patterns concordant with endemism richness are important since intensification processes are likely to have an array of effects on biodiversity (Donald *et al.*, 2001; Benton *et al.*, 2003; Kerr & Cihlar, 2004; Yamaguchi & Blumwald, 2005; Herzon *et al.*, 2008; Flynn *et al.*, 2009; Gibbs *et al.*, 2009; Kleijn *et al.*, 2009; Alkemade *et al.*, 2010; Felton *et al.*, 2010; Alkemade *et al.*, 2012). Intensification processes are also likely to influence birds, mammals and amphibians in various ways. While broad patterns were overall remarkably similar, the results highlighted some differences in the detail. Unique taxon-specific areas associated with high LUI were highlighted for amphibians in the South-eastern U.S., mammals in the Caucasus, amphibians and mammals in Europe and birds in Latin America and Australia. Such differences among taxonomic classes are of interest as they suggest a limited usefulness of surrogate taxa on a global scale.

Of our thirteen LUI metrics, eight were related to the yield and yield gaps of different crops, therefore it is not surprising that different patterns concordant with high endemism richness

emerge. However, the differences that we find in high intensity land-use, not just between yields but also in the inputs involved in increasing yields are diverse. We thus highlight not only where different crops are grown intensively alongside biodiversity, but also the concordance of biodiversity and the high intensity management processes behind such yields.

The land sharing-sparing debate sparked a wider appreciation of LUI with regard to yields (Green *et al.*, 2005; Phalan *et al.*, 2014). The use of yields alone is logical when focusing on increased agricultural production; however, this approach does not give us clear insights into which management practises have resulted in yield increases. While our study does not provide insights into the relative impact of intensification vs. expanding agricultural area, our results do show that a focus on yields or yield gaps alone will likely be insufficient to assess the biodiversity impact of agriculture. This is particularly relevant, given that some forms of management may threaten biodiversity more than others (e.g., conventional vs. organic agriculture), and some farming practices (e.g., agro-ecological farming, Perfecto & Vandermeer, 2010) may even lead to co-benefits in terms of biodiversity. Similarly, studies which focus exclusively on habitat loss or other single LUI metrics, such as fertilisers (Kleijn *et al.*, 2009) or human population density as a proxy for LUI (Pekin & Pijanowski, 2012) could lead to incomplete or biased conclusions when identifying priority areas for biodiversity conservation.

The incongruence of CI hotspots and regions of high LUI and high endemism richness further highlights this. Although the total area of high LUI and high endemism richness was slightly greater than the total area of CI hotspots, many large regions had no overlap. Considering the various negative effects intensification can have on biodiversity, such areas which were not covered by CI hotspots may merit more attention with a combination of relevant LUI metrics investigated accordingly. All regions where the top 2.5% of LUI and endemism richness overlapped were within CI hotspots. Thus, despite the incongruence of CI hotspots and regions of high LUI and endemism richness from the LISA analysis, when LUI is particularly intense (top 2.5%) the two distributions converge. This may, in part, be because in regions with particularly high LUI, some of the conditions used to define CI hotspots are met (e.g., 70% of native habitat lost). It should also be noted that the majority of the globe's land area (79%) was highlighted by one or more other global conservation priority schemes, and that our regions of high LUI associated with high endemism richness are covered by several of these schemes (e.g., Papua New Guinea is included in High

Biodiversity Wilderness Areas, Venezuela and China by Megadiversity Countries, and Eastern Africa by the Global 200 Ecoregions, see Brooks *et al.*, 2006).

In debates addressing broad topics such as sustainable intensification and biodiversity conservation, we recommend a more multidimensional approach to agricultural intensification, where relevant LUI metrics are included in accordance with research goals. Areas with high yield gaps and high endemism richness may represent potential future conflicts between high LUI and biodiversity. In less developed regions with high biodiversity, intensification can be limited by a lack of capital investment and access to resources (Mueller *et al.*, 2012). However, foreign investment spurred by increasing land scarcity is increasing (Rulli *et al.*, 2013). For example, high cropland cover and HANPP now dominate in Southeast Asia, where the area of palm oil cultivation has increased by 87% in the last decade (FAOSTAT, 2010) and is one of the biggest threats to biodiversity in the region (Wilcove *et al.*, 2013). Considering the detrimental effects of using increased inputs such as fertiliser and pesticide on biodiversity (Kerr & Cihlar, 2004; Gibbs *et al.*, 2009), the various forms of intensification that are possible in these regions may result in considerable biodiversity threat and conservation conflicts. It should also be noted that areas shown here where future intensification may occur are based only on current low-intensity regions which may not necessarily become high intensity in the future due to many reasons such as poor soil quality, rugged topography, or climate constraints.

With a growing consensus that both expansion and intensification are likely to continue in the future, investigating which areas should be prioritised for sustainable intensification or nature protection becomes central to conservation research (Green *et al.*, 2005; Phalan *et al.*, 2014). One potential avenue may be to concentrate intensification strategies in coldspots of low intensity and low biodiversity, therefore increasing yields while minimizing costs to biodiversity. Another, complementary pathway to lessen negative biodiversity impacts of intensification is by reducing overuse of fertilisers and irrigation in over-saturated areas (e.g., China and parts of Europe), while allowing for more fertiliser use in less productive areas (Mueller *et al.*, 2012). However, we strongly caution that detailed, context-specific assessments of the possible outcomes of different intensification strategies on the various aspects of biodiversity at the local-to-regional scale are needed for such analyses, accompanied with an assessment of other socio-ecological outcomes, as coldspot regions may include both valuable and endemic biodiversity and cultural heritage that intensification may threaten. While our results are coarse in scale and cannot reveal specific areas for

sustainable intensification, we do offer a starting point for identifying areas of current and potentially suitable future intensification.

We compiled a set of LUI metrics with the highest spatial resolution currently available. Nevertheless, despite considerable recent progress, numerous gaps exist regarding the availability of alternative indicators and the difficulties in their measurement related to issues with data availability, accuracy, and error propagation (Kuemmerle *et al.*, 2013). With many inconsistent definitions in the literature, conceptually framing LUI is challenging (Kuemmerle *et al.*, 2013). Uncertainties in the accuracy of current LUI maps are often high due to inconsistent input data and limitations with processing algorithms and positional accuracy which is exacerbated by a lack of formal validation (Verburg *et al.*, 2011). Systematically collected ground-based data only covers a few regions of the globe, statistical data are often only available at the national scale, and remote sensing cannot easily capture the subtle spectral effects of LUI changes (Kuemmerle *et al.*, 2013). Many LUI maps used here are based on one cropland hybrid map (Panel SI II-1, Ramankutty *et al.*, 2008) and inaccuracies in the base map can propagate onto derivative maps (Verburg *et al.*, 2011; Table SII-1). This partly explains, for example, the large correlation found between fertiliser and cropland extent (0.92, Table SI II-3). However, higher correlations were found between taxonomic classes, highlighting the variety in spatial patterns of LUI metrics.

Information on mining, pesticide use, shifting cultivation, frequency of fire grazing, labour intensity, mechanisation, intensity of wood felling, and field sizes was still too limited to be included in this research. Furthermore, time series for LUI datasets are currently not available but would be desirable as they could allow for causal analysis. Global data relevant to broader socioeconomic processes are also lacking (Otto *et al.*, 2015).

In terms of biodiversity, we included just one global-scale measure. We chose endemism richness as it combines species richness and endemism (Figure SI II-8) and thus indicates the relative importance of a grid cell for species conservation on a global scale (Kier *et al.*, 2009). This is an advantage over species richness which is often representative of common, widespread species that can overshadow rare or small-ranged species, often in need of conservation (Grenyer *et al.*, 2006). Considering a more diverse range of biodiversity metrics may provide a richer view of patterns of LUI and biodiversity. However, since the main aim of this study was to compare the patterns of numerous LUI metrics concordant with biodiversity, and because a relatively large body of work has already been carried out on the differences between and the complexity of biodiversity metrics (Grenyer *et al.*, 2006; Kier

*et al.*, 2009), we used only one measure of biodiversity. Future studies could consider a wider set of metrics, including information on abundance, functional, phylogenetic, or beta-diversity. The inclusion of measures of ecosystem services, resilience, extinction debt (Essl *et al.*, 2015) and societal outcomes could also prove beneficial.

The paucity of readily available species occurrence data is a major impediment in mapping global patterns, with notably less data available for less charismatic species and less developed countries, which is where most biodiversity is thought to occur. High potentials for yield improvements are often found in lesser studied regions in the tropics (Mueller *et al.*, 2012) thus making the possible land-use threat to biodiversity even hazier. While species distribution data scaled to a finer resolution than 110 x 110 km is available, a substantial mismatch of global-scale range-map distributions with species' actual distributions occurs at finer scales, resulting in an overestimation of species occurrences (Hurlbert & Jetz, 2007). Therefore, at the current resolution, the exact configuration of land uses within each grid cell cannot be accounted for. This resolution is also likely to oversimplify fine-scale patterns of concordance of LUI and biodiversity, and differences between taxonomic classes. This has implications for what is in reality a LUI-biodiversity hotspot but has been missed as a hotspot due to taking the average LUI values per grid cell i.e. a grid cell may contain both very high and very low LUI but is represented here as medium LUI due to averaging. Furthermore, the same data can produce different results when aggregated in different ways – this is applicable to any zoning of spatial units and is known as the modifiable areal unit problem (Openshaw & Taylor, 1979; Jelinski & Wu, 1996). Together, these issues represent limitations for studying the effect of LUI on biodiversity.

## **5 Conclusions**

Considering the increasing demand for food and bioenergy production, understanding the pressure land-use change exerts on biodiversity is crucial. In the past, such assessments have predominately focused on the extent of land use. However, intensification has been a major mode of land-use change historically (Rudel *et al.*, 2009) and is likely to continue due to economic pressure and government policies to intensify agriculture in less developed, yet highly biodiverse areas (van Vliet *et al.*, 2012). Different LUI metrics highlight different high-pressure regions, suggesting conservation research should embrace the multiple aspects of LUI and include relevant intensity metrics when considering biodiversity threat. This is particularly important since most global assessments of the land-use impact on biodiversity,

as well as the current land sparing vs. land sharing debate, have at best relied on single measures of LUI (Ellis & Ramankutty, 2008; Kleijn *et al.*, 2009; Pekin & Pijanowski, 2012). We identify areas of particularly high endemism richness and high LUI and thus shed light on regions of potential conflict where highly intensive agriculture and unique biodiversity coincide.

Our research provides a starting point to investigate the relationship between the many facets of intensification and biodiversity, and to explore regions that could pose a threat to biodiversity if intensification were to occur. In general, expansion and intensification processes aim to address the growing demand for resources, but both can have negative effects on biodiversity and neither can provide an all-encompassing solution if the root drivers of biodiversity loss are not tackled. Successful conservation strategies should consider population growth, overconsumption of meat and dairy, food wastage and distribution, and defective socio-economic, institutional and political systems not as uncontrollable factors, but as opportunities for change and improvement. Tackling these root causes of land-use change and subsequent biodiversity loss can reduce the pressure currently seen on biodiversity and aid in meeting the great challenge of increasing food availability to feed a growing world population, and at the same time, preserve remaining wildlife.

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## Supplementary Information

### Panel SI II-1 Bibliography of datasets used for Endemism Richness and LUI metrics

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  10. Wint, W. & Robinson, T. (2007) Gridded livestock of the world. In, p. 131. Food and Agriculture Organization of the United Nations (FAO), Rome – Table SI II-1 Output Metric (b). (see reference 8 for an updated publication on livestock densities)
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Table SI II-1: Details on datasets of LUI metrics

	<i>Dataset</i> <i>(citation, original scale, year)</i>	<i>Description</i> <i>(data value, reference year)</i>	<i>Data Source</i>
<i>INPUT METRICS</i>	<b>(a.) Cropland extent</b> (Ramankutty et al., 2008, 5min, 2000, Panel SI II-2 ref. 7)	(% per grid cell, 1997–2003)	FAO, national inventories and MODIS global land cover and GLC2000.
	<b>(b.) Land equipped for irrigation</b> (Siebert et al., 2005, 5min, 2000, Panel SI II-3 ref 9)	(% per grid cell, ~2000)	FAO, World Bank, <a href="#">USGC-GLCC-2.0</a> and <a href="#">JRC-GLC2000</a> land cover datasets used when no other spatial info available.
	<b>(c.) Industrial &amp; manure fertilizer application rates</b> (N, P) (Potter et al., 2010, 10km, 2000, Panel SI II-4 ref 6)	Nitrogen fertilizer nutrients applied to croplands (kg/ha, 1994-2001).	FAO “Fertilizer Use by Crop 2002” combined with harvested area for 175 crops (Monfreda et al. 2008).
			Combining census statistics with global cropland area (Ramankutty et al. 2008)
<i>OUTPUT METRICS</i>			FAO and spatially predicted on suitable land
<i>SYSTEM METRICS</i>	<b>(a.) HANPP</b> (Haberl et al., 2007, 5 min, 2000, Panel SI II-7 ref 2)	Human Appropriated Net Primary Productivity (per cent of NPP0, 2000)	FAO and Lund–Potsdam–Jena (LPJ) DGVM (18, 19) global vegetation models
	<b>(b.) Yield Gaps -</b> Wheat, maize and rice yield gap (Neumann et al., 2010, 5min, ~2000, Panel SI II-8 ref 5)	Yield gaps here refer to the difference between the actual yield and estimated frontier yield ** (t/ha, ~2000)	Global data on actual grain yields were obtained from Monfreda et al. (2008) potential yield calculated by integrating biophysical and land management-related factors.

\* Harvested area was chosen for soybeans and palm oil as its spatial pattern more closely resembled previously published data on yields and harvested area (Fitzherbert *et al.*, 2008; GAEZ, 2010; Ray *et al.*, 2012; Ray *et al.*, 2013a; USDA, 2013) than the yields dataset by Monfreda et al. (2008). Furthermore, in areas of intensive soy and palm oil production, biodiversity is generally low when compared to other land covers (Mattsson *et al.*, 2000; Fearnside, 2001; Fitzherbert *et al.*, 2008; Koh & Wilcove, 2008).

\*\* Yield gaps can also be measured as the proportion of actual and potential yield. However, when measured in this way, areas with similar proportional yield gaps are indistinguishable from each other - e.g., two areas may have a relative yield gap of 50%, but the first has a yield of 1 t/ha and an attainable yield of 2 t/ha, the other a yield of 15 t/ha and an attainable yield of 30 t/ha. Here, the second area holds a much greater potential for producing more food by closing this gap. These are the areas of particular interest in the sustainable intensification debate and so we have chosen this measure for the purpose of this paper. Note that this measure has its own shortfall in that it does not give us information on the original attained yield as the proportional yield gap does, however, one single measure could not cover all aspects of yield gaps.

Table SI II-2: Average percentile ranks for LUI and Endemism Richness in top 2.5% hotspots. Higher percentile ranks indicate higher values. For example, a percentile rank of 70 indicates that the metric is higher than 70 per cent of the overall distribution of that indicator. Inverse yield gaps are given in brackets.

	Mammal	Bird	Amphibian	Cropland	Fertilizer	Irrigation	HANPP	Rice Y. (Gap)	Maize Y. (Gap)	Wheat Y. (Gap)	Livestock	Soy	Palm Oil
<b>Mexico</b>	90	90	90	90	0	0	80	20(0)	20(0)	20(0)	30	90	40
<b>Cuba</b>	80	90	90	80	0	90	80	50(60)	40(0)	0(0)	80	0	0
<b>Haiti</b>	80	90	90	90	60	50	90	50(10)	30(10)	0(0)	90	0	0
<b>Northern Andes</b>	90	90	90	50	70	60	70	70(80)	60(70)	30(0)	90	20	60
<b>Central Andes</b>	90	90	80	50	60	60	60	90(0)	70(70)	60(0)	80	0	0
<b>Southern Andes</b>	90	90	90	70	60	90	60	0(0)	60(60)	30(80)	50	0	0
<b>Atlantic Forest</b>	90	90	90	60	60	40	80	80(70)	60(30)	0(0)	90	0	0
<b>Afromontane</b>	90	90	90	70	50	40	80	50(90)	60(40)	60(90)	90	20	10
<b>Western Ghats</b>	90	90	90	90	70	80	90	80(70)	40(60)	10(0)	90	0	0
<b>Indochinese Region</b>	90	90	90	80	90	60	90	80(50)	60(70)	50(80)	80	60	10
<b>Borneo</b>	90	90	80	90	90	0	70	20(20)	10(0)	0(0)	50	0	90
<b>Java</b>	90	90	90	90	90	80	90	80(80)	60(30)	0(0)	80	80	70
<b>Sulawesi</b>	90	90	70	90	40	0	70	40(50)	30(30)	0(0)	60	70	0
<b>Philippines</b>	90	90	90	90	80	90	90	60(30)	50(10)	0(0)	60	0	70
<b>Australia</b>	90	90	90	50	50	50	60	0(0)	60(0)	50(0)	90	60	0

Table SI II-3: Spearman's rank correlation coefficients of all LUI, Endemism and Species Richness datasets. With the exception of Wheat Yield and Palm Oil HA (shown in grey), all correlations were statistically significant at the  $p < 0.05$  level.

	ER Mam.	ER	ER Amp.	SR Mam.	SR Bird	SR Amp	Crop	Fert.	Irr.	Livestock	HAN-PP	Wheat Y.	Maize Y.	Rice Y.	Inv. Wheat Gap	Inv. Maize Gap	Inv. Rice Gap	Soy HA	Palm Oil Ha
ER Mam	1.00																		
ER Birds	0.95	1.00																	
ER Amp	0.89	0.90	1.00																
SR Mam	0.89	0.88	0.85	1.00															
SR Birds	0.90	0.93	0.89	0.96	1.00														
SR Amp	0.84	0.87	0.97	0.93	0.93	1.00													
Cropland	0.71	0.71	0.72	0.74	0.77	0.73	1.00												
Fertiliser	0.67	0.68	0.69	0.70	0.74	0.70	0.92	1.00											
Irrigation	0.45	0.44	0.47	0.46	0.49	0.46	0.68	0.69	1.00										
Livestock	0.77	0.79	0.78	0.80	0.83	0.79	0.85	0.84	0.65	1.00									
HANPP	0.73	0.74	0.76	0.75	0.79	0.76	0.86	0.83	0.68	0.89	1.00								
Wheat Y.	0.54	0.55	0.55	0.58	0.59	0.55	0.80	0.79	0.66	0.73	0.71	1.00							
Maize Y.	0.70	0.69	0.70	0.71	0.77	0.71	0.88	0.84	0.64	0.78	0.77	0.77	1.00						
Rice Y.	0.64	0.66	0.66	0.66	0.65	0.65	0.65	0.54	0.45	0.55	0.55	0.44	0.66	1.00					

Chapter II

Inv. Wheat Gap	0. 2 0	0. 1 5	0. 2 0	0. 2 5	0. 2 3	0. 2 0	0. 4 9	0. 4 8	0. 4 4	0. 4 0	0. 4 3	0. 5 0	0. 4 3	0. 1 7	1. 0 0					
Inv. Maize Gap	0. 3 4	0. 3 5	0. 3 7	0. 3 7	0. 3 9	0. 3 9	0. 4 7	0. 4 6	0. 3 9	0. 4 4	0. 4 3	0. 3 8	0. 4 7	0. 4 2	0. 2 5	1. 0 0				
Inv. Rice Gap	0. 3 1	0. 3 3	0. 3 3	0. 2 8	0. 3 1	0. 3 1	0. 3 7	0. 3 7	0. 3 6	0. 3 5	0. 3 6	0. 1 9	0. 3 2	0. 5 0	0. 0 9	0. 3 7	1. 0 0			
Soy HA	0. 3 8	0. 3 8	0. 4 3	0. 4 5	0. 4 6	0. 4 6	0. 6 2	0. 6 1	0. 5 2	0. 5 6	0. 5 7	0. 5 5	0. 6 5	0. 4 6	0. 3 8	0. 4 8	0. 3 7	1. 0 0		
Palm Oil Ha	0. 3 3	0. 3 4	0. 3 2	0. 3 2	0. 3 2	0. 3 2	0. 2 4	0. 1 7	0. 0 2	0. 1 4	0. 1 8	0. 0 1	0. 2 1	0. 3 6	0. 0 9	- 0. 4	0. 1 2	0. 2 2	0. 0 8	1. 0 0

Figure SI II-1: Top 2.5, 5, and 10% of LUI metrics. (a.) cropland extent, (b.) fertilizer, (c.) irrigation, (d.) palm oil, (e.) soy, (f.) livestock, (g.) rice, (h.) wheat, (i.) maize, (j.) yield gap rice, (k.) gap wheat, (l.) gap maize, (m.) HANPP. Note, inverse yield gaps (j-k) shown in red, top 2.5%, orange, top 5%, yellow top 10% indicate potential for intensification, high intensity (i.e. low yield gaps) is indicated in purple.

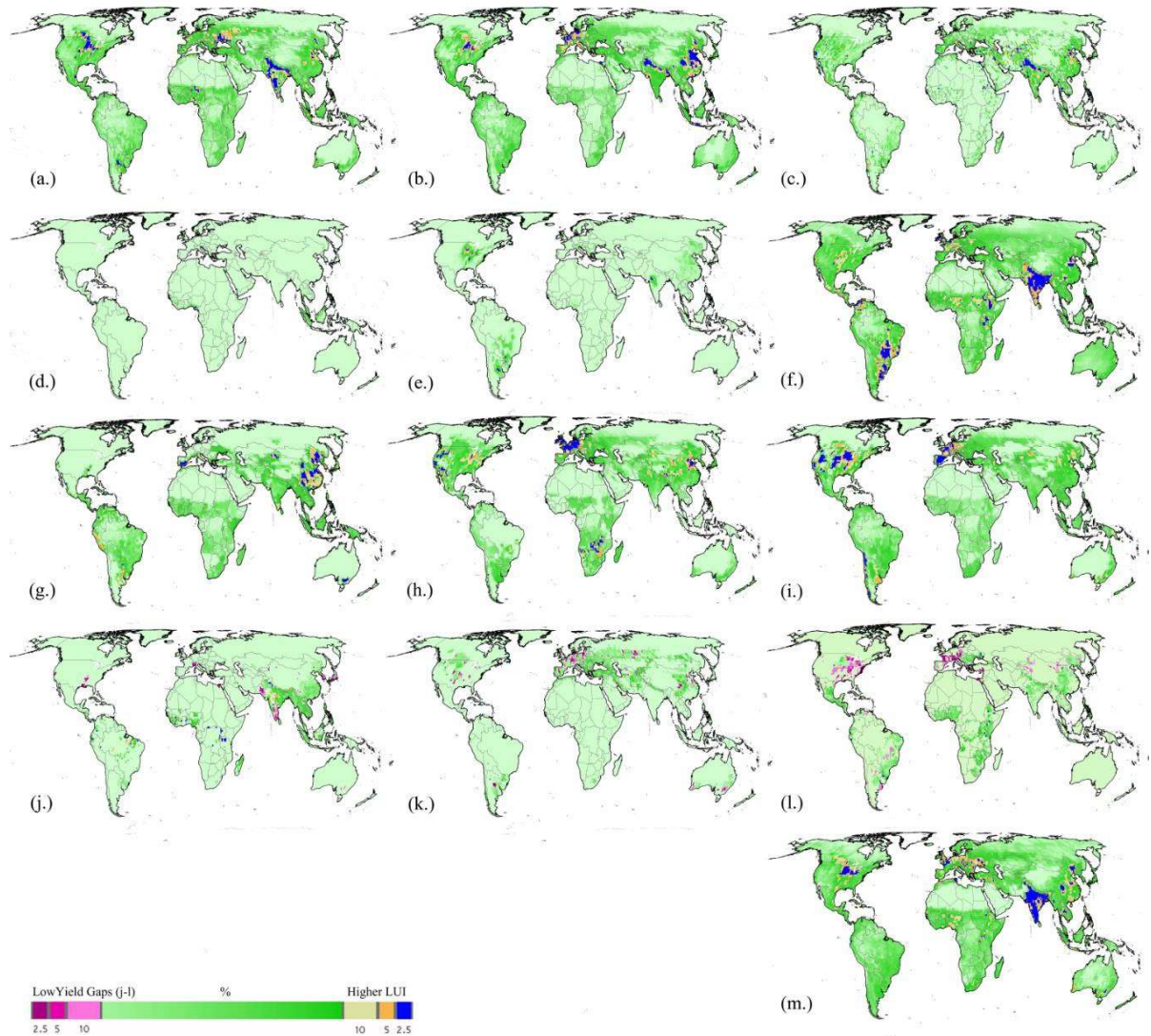


Figure SI II-2: Top 2.5, 5, and 10% of Endemism Richness for (a.) mammals, (b.) birds and (c.) amphibians

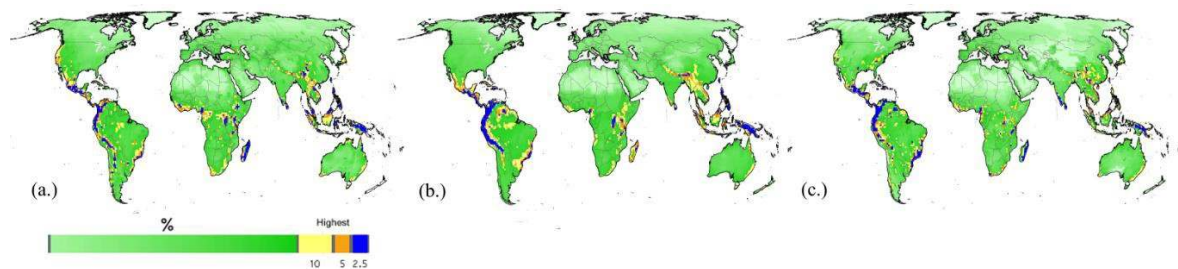
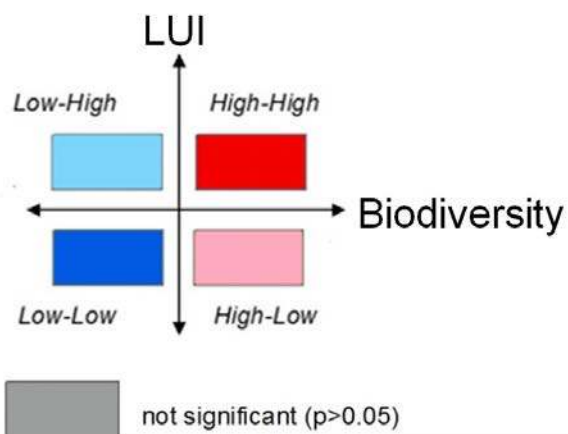
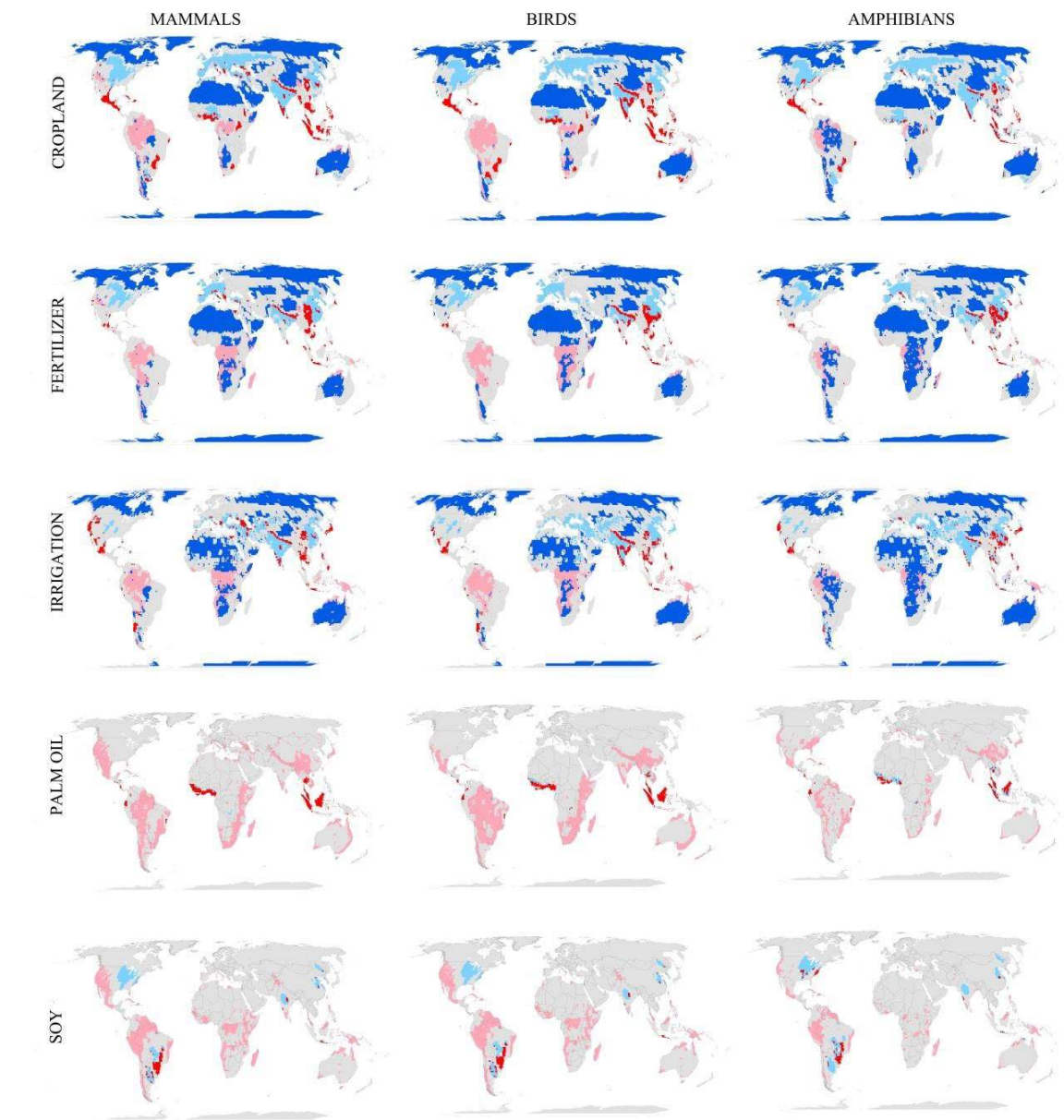
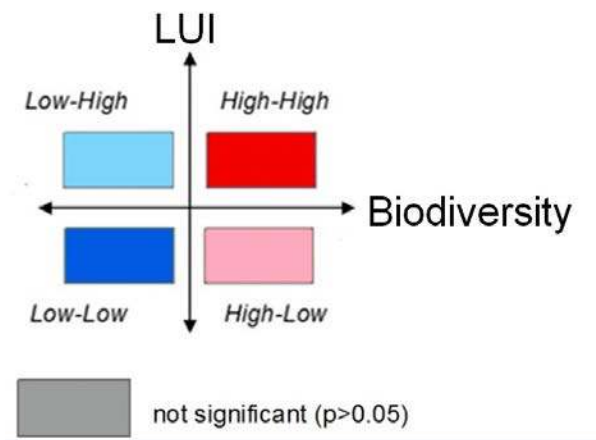
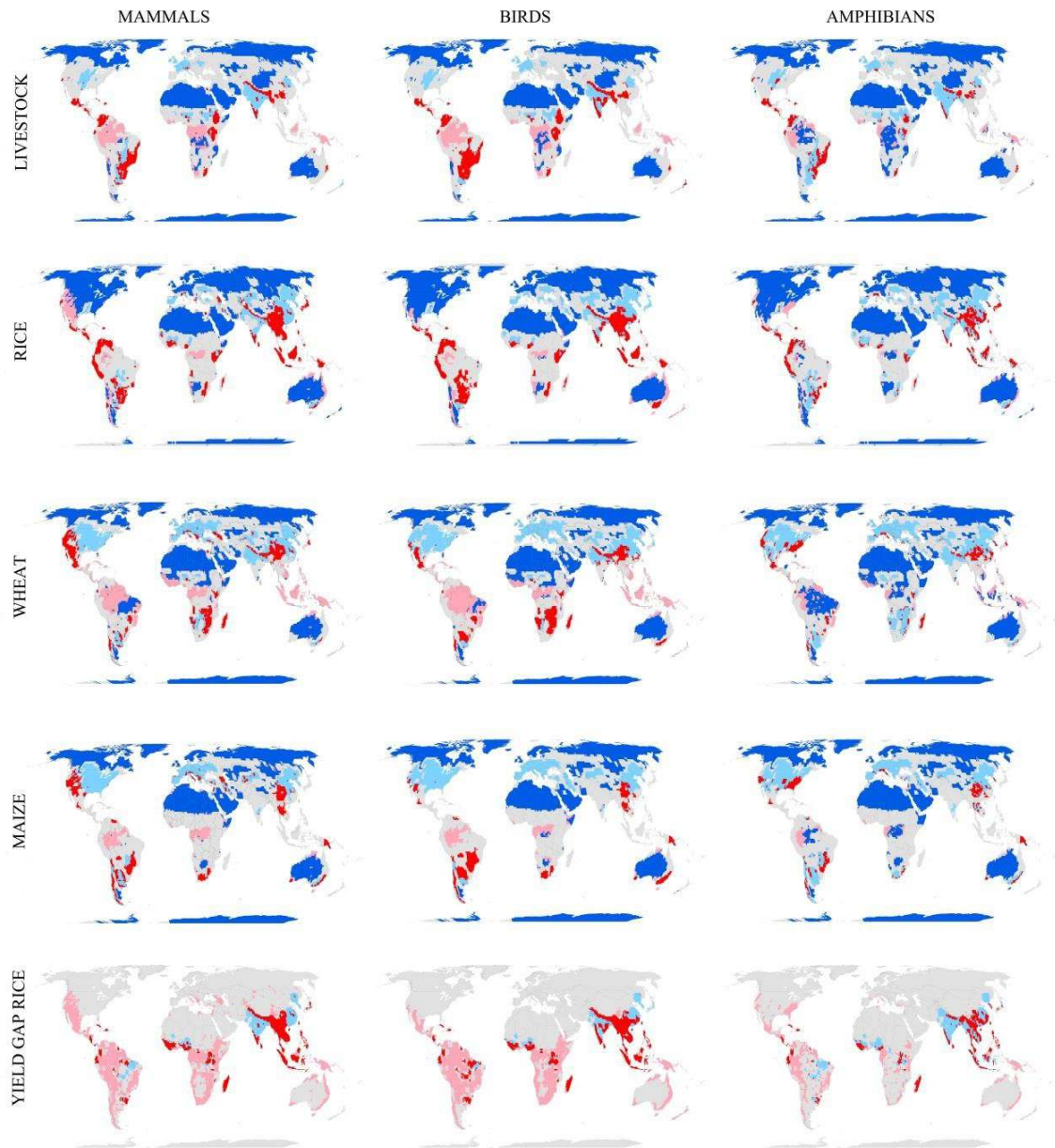


Figure SI II-3: Individual LISA results for each LUI metric and Endemism Richness. This analysis indicates the spatially-explicit strength of associations between two variables and results in (1) high-high values, here, where high biodiversity is surrounded by high land-use intensity (in red), (2) high-low values, high biodiversity surrounded by low LUI (in pink), (3) low-high, low biodiversity surrounded by high LUI (in light blue), and (4) low-low, low biodiversity surrounded by low LUI (in dark blue). Note, yield gaps are inverse so higher values indicate higher LUI (low yield gaps).







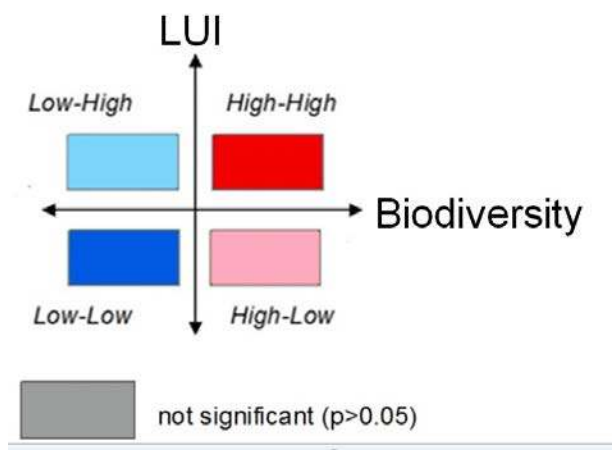
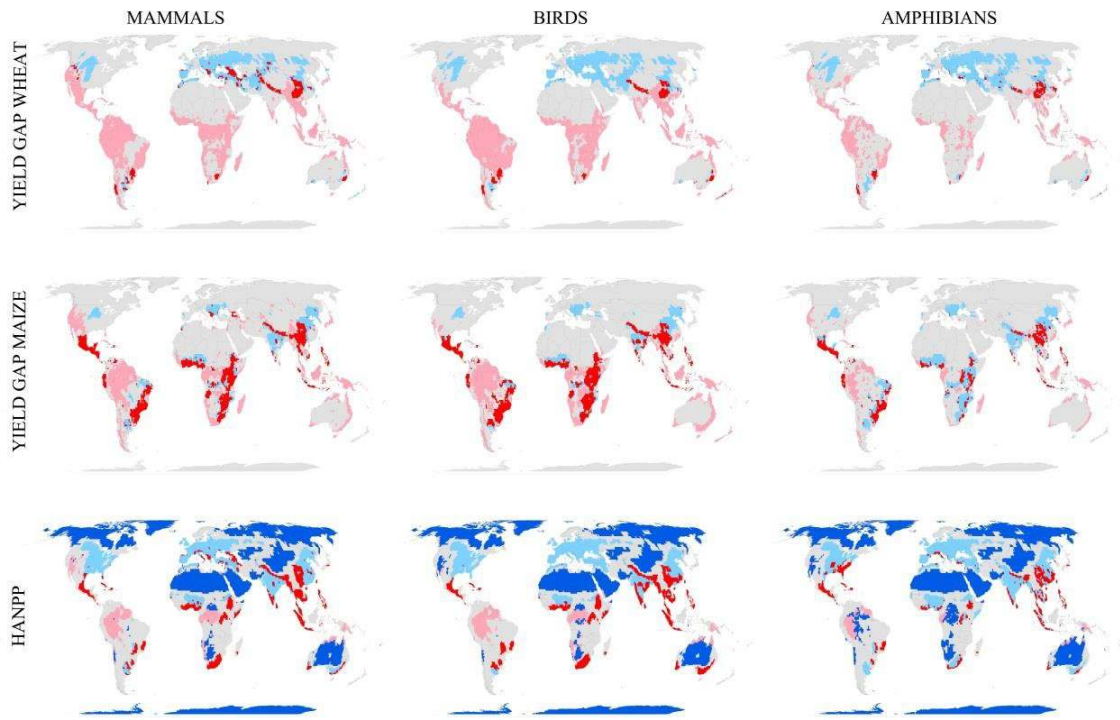




Figure SI II-4: (a) Areas of low Endemism Richness and high LUI and (b) high Endemism Richness surrounded by low LUI areas according to statistically significant ( $p < 0.05$ ) LISA results. We show areas where biodiversity is high for all three taxonomic classes (in blue), any two taxonomic classes (in green) and 1 taxon (in yellow) concordant with (a) a minimum of one high land-use intensity indicator and (b) a minimum of one indicator of low intensity land-use. A low intensity land-use indicator gives us an idea of areas of potential future threat if intensification were to occur. Note: in such areas, low intensity can relate to as few as one intensity metric at a low value concordant with biodiversity, other intensity indicators may already be high in the same region (see Figure II-1).

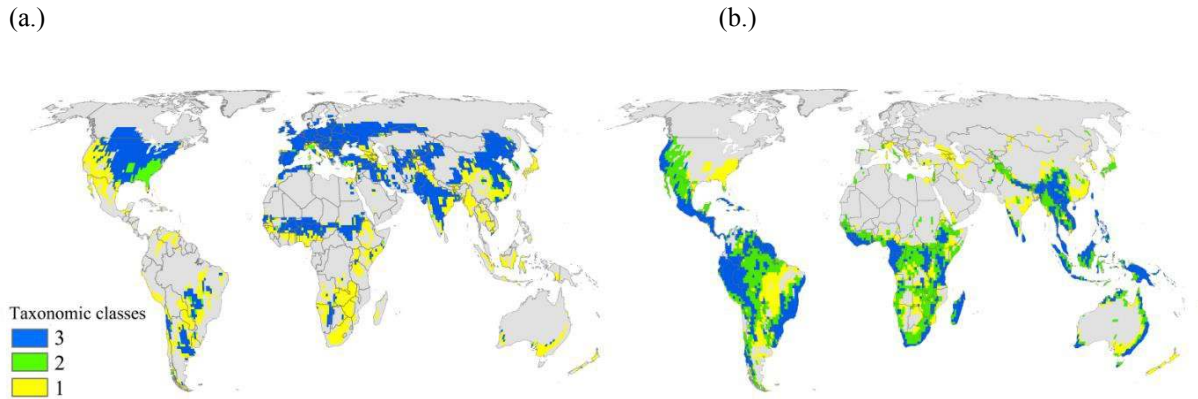


Figure SI II-5: Percentage of ecozone containing regions of high Endemism Richness and high LUI from LISA analysis ( $p < 0.05$ ). Note: areas are over entire grid cells, specific configurations within grid-cells are not known.

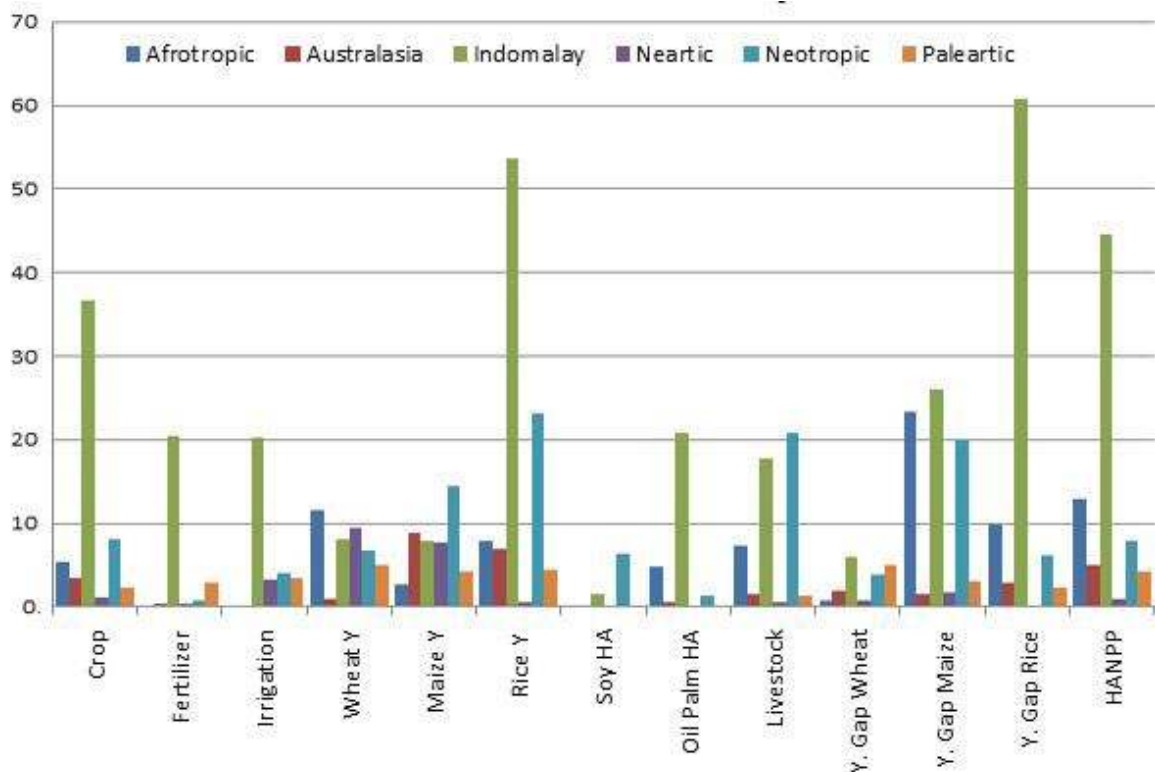


Figure SI II-6: Areas where high LUI (combined for input, output and system metrics) is associated with high Endemism Richness (for each taxonomic class) from LISA analysis. Note: Yield gaps are inverted so high numbers relate to high LUI. Purple areas indicate more than one intensity metric.

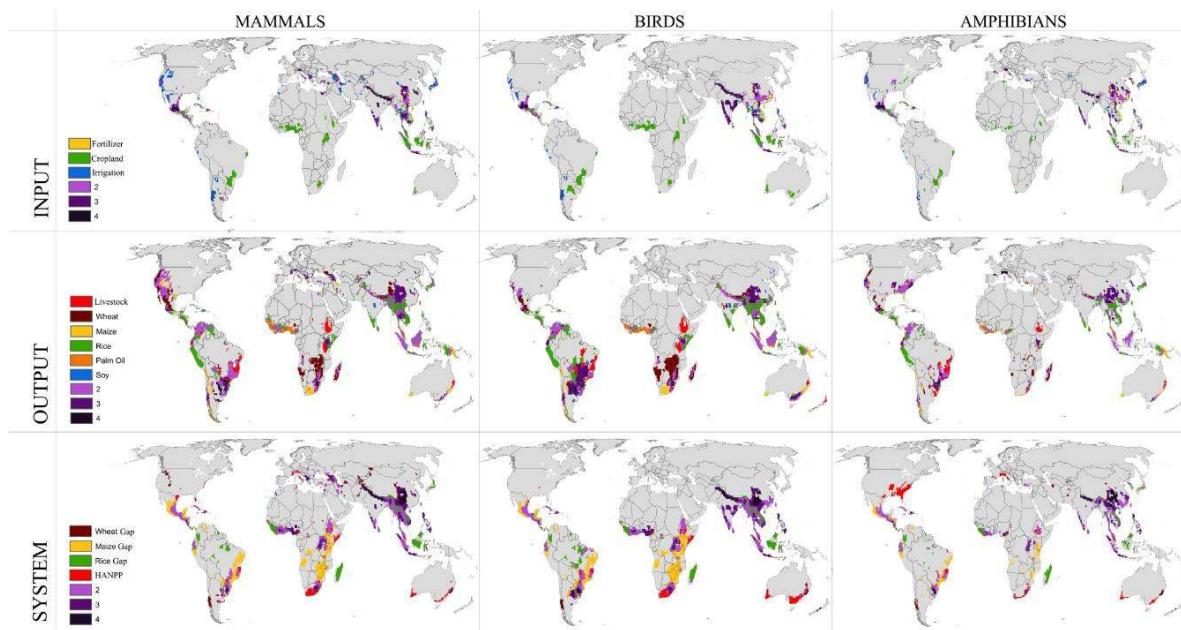


Figure SI II-7: Regions of high land-use intensity (LUI) and high endemism richness for mammals, birds and amphibians (in blue) compared to CI hotspots

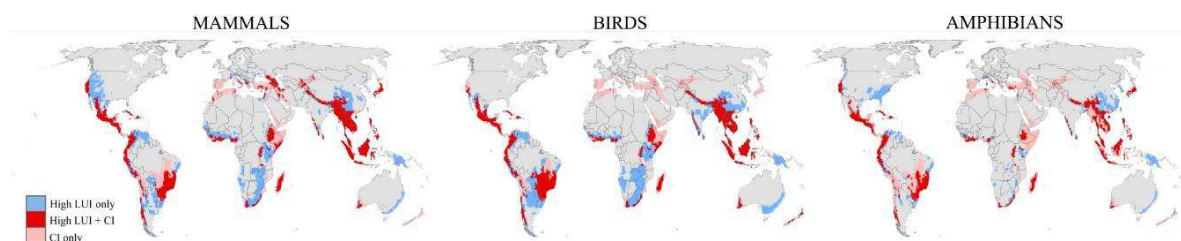
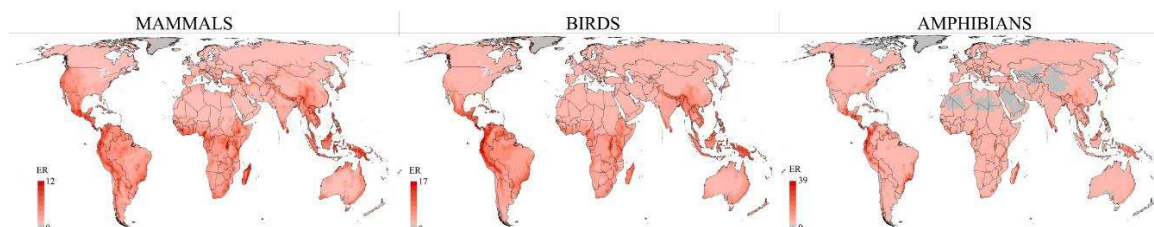


Figure SI II-8: Endemism Richness for mammals, birds and amphibians







**Chapter III:**  
**Agriculture rivals biomes in predicting global  
species richness**  
*Ecography, 2016 (in press)*

Laura Kehoe, Cornelius Senf, Carsten Meyer, Katharina Gerstner,  
Holger Kreft, and Tobias Kuemmerle

## **Abstract**

Species-area relationships (SARs) provide an avenue to model patterns of species richness and have recently been shown to vary substantially across regions of different climate, vegetation, and land cover. Given that a large proportion of the globe has been converted to agriculture, and considering the large variety in agricultural management practices, a key question is whether global SARs vary across gradients of agricultural intensity.

We developed SARs for mammals that account for geographic variation in biomes, land cover and a range of land-use intensity indicators representing inputs (e.g. fertilizer, irrigation), outputs (e.g. yields) and system-level measures of intensity (e.g. human appropriation of net primary productivity - HANPP). We systematically compared the resulting SARs in terms of their predictive ability.

Our global SAR with a universal slope was significantly improved by the inclusion of any one of the three variable types: biomes, land cover, and land-use intensity. The latter, in the form of human appropriation of net primary productivity (HANPP), performed as well as biomes and land-cover in predicting species richness. Other land-use intensity indicators had a lower predictive ability.

Our main finding that land-use intensity performs as well as biomes and land cover in predicting species richness emphasizes that human factors are on a par with environmental factors in predicting global patterns of biodiversity. While our broad-scale study cannot establish causality, human activity is known to drive species richness at a local scale, and our findings suggest that this may hold true at a global scale. The ability of land-use intensity to explain variation in SARs at a global scale had not previously been assessed. Our study suggests that the inclusion of land-use intensity in SAR models allows us to better predict and understand species richness patterns.

## 1 Introduction

The species-area relationship (SAR) is one of the most robust patterns found in ecology (Rosenzweig, 1995) and is crucial to our understanding of biodiversity patterns (Rosenzweig, 1995; Turner & Tjørve, 2005; Drakare *et al.*, 2006; Dengler, 2009). By relating the number of species to the area of habitat, the application of SARs is central in predicting species loss in areas of habitat loss and land-use change (Ladle & Whittaker, 2011; Keil *et al.*, 2015). A key step in SAR analyses is to accurately estimate the slope of the relationship, i.e. the rate of species loss related to area loss. However, applying a universal (canonical) slope and treating human-dominated land as inhospitable (Pimm *et al.*, 1995; Brooks *et al.*, 2002; Thomas *et al.*, 2004) may be overly simplistic since SAR slopes are known to vary geographically (Drakare *et al.*, 2006; Gerstner *et al.*, 2014) and since numerous factors may allow for species survival in the matrix surrounding remaining habitat patches.

A complex interplay of ecological, evolutionary, and environmental factors influences species richness in a given area. For example, the importance of energy availability and ecosystem productivity in predicting species richness has led to the development of the species-energy theory (Wright, 1983), whereby, at broad scales, a positive relationship is generally found for terrestrial vertebrates, where higher energy availability results in higher species richness (Currie, 1991; Gaston, 2000; Cusens *et al.*, 2012). Other factors that can influence species richness in a given area include dispersal ability (Storch *et al.*, 2005), evolutionary history (Belmaker & Jetz, 2015), disturbance frequency, climate (Hawkins *et al.*, 2003b; Kreft & Jetz, 2007) and environmental heterogeneity (Stein *et al.*, 2014).

Many of the natural bioclimatic factors at play in driving species distributions and species richness may be summed up by biome classifications. This is because biomes represent major types of potential natural vegetation originating from distinct climatic conditions (Olson & Dinerstein, 1998; Ladle & Whittaker, 2011). Land cover has many similarities with biome classifications, as land cover represents the biophysical attributes of the land surface (Lambin *et al.*, 2001) and is determined by the climate, topography, and soil. Land cover additionally includes areas predominantly influenced by human activity such as croplands.

Agricultural expansion leading to land-cover conversions is one of the main drivers of species loss on a global scale (Sala *et al.*, 2000; Pereira *et al.*, 2012), but species also respond differently to habitat loss and degradation (Pereira & Daily, 2006). Recent studies reflect this, for instance, through the development of matrix-calibrated SARs which incorporate land-cover change (Koh & Ghazoul, 2010), and SARs which include species specific

habitat-affinity in human-modified landscapes (Pereira & Daily, 2006). Countryside biogeography also provides better insights into species survival in complex agricultural landscapes and forest fragments (Mendenhall *et al.*, 2014).

While currently available land-cover datasets (Channan *et al.*, 2014) and SAR models incorporating land use (Pereira & Daily, 2006; Koh & Ghazoul, 2010) distinguish between natural or agricultural land-cover types, land-management practices can differ greatly in what we broadly describe as agricultural land. In parallel to agricultural expansion leading to land-cover conversions, agriculture has also rapidly intensified since the 1950s. For example, global irrigated areas have doubled in size (FAOSTAT, 2010) and fertilizer application has increased fivefold (Matson *et al.*, 1997; Tilman *et al.*, 2001).

This is problematic because high agricultural land-use intensity (LUI) is generally detrimental to local species richness and abundance (Newbold *et al.*, 2015). However, despite the global increase in LUI, most studies investigating land use and biodiversity are local in scale and either disregarded LUI completely or used only a single metric to measure it (Herzon *et al.*, 2008; Kleijn *et al.*, 2009; Geldmann *et al.*, 2014). The latter approach has been shown to be simplistic as LUI is a multidimensional concept that embodies a wide variety of management practices that can have diverse effects on biodiversity. For instance, fertilizers and pesticides pose a substantial threat to terrestrial vertebrates (Kerr & Cihlar, 2004; Gibbs *et al.*, 2009; Kleijn *et al.*, 2009). Long-term irrigation can salinize soils which can eventually become toxic to plants with potentially detrimental effects to entire ecosystems (Yamaguchi & Blumwald, 2005). Intensive livestock grazing can have negative effects on biodiversity (Alkemade *et al.*, 2012) and ecosystems, especially in the absence of remnant vegetation (Felton *et al.*, 2010). All of these effects are of particular concern since different combinations of high LUI concordant with high biodiversity are spread heterogeneously across the globe (Kehoe *et al.*, 2015) and may have region-specific effects on biodiversity. Therefore, while it is generally not accounted for, the intensity of agricultural land use may improve predictions of SARs in human-modified landscapes.

While the inclusion of biomes and land cover has recently been shown to improve SAR predictions for plants on a global scale (Gerstner *et al.*, 2014), it remains unclear whether this extends to other taxa, and whether the inclusion of measures of land-use intensity improves global SAR models. Furthermore, the importance of human influence on species richness is often embraced at local grains (Dornelas *et al.*, 2014; Newbold *et al.*, 2015), however, recent research is emerging that indicates broader patterns of species richness



might also be related to human activities more than we suspect (Murray & Dickman, 2000; Di Marco & Santini, 2015).

Here, we first evaluated the extent to which the inclusion of agricultural activity and management in the form of land cover and land-use intensity improves global SAR models. To account for the multidimensionality of land-use intensity, we assessed three broad categories of agricultural management metrics, representing input (the intensity of land use along different input dimensions, e.g. fertilizer and irrigation), output (the ratio of outputs from agricultural production, e.g. yields, t/ha/yr) and system metrics (the relationship between the inputs or outputs of land-based production to the overall system, e.g. human appropriation of NPP). Following this step, we compared whether this improvement is comparable to the inclusion of climate conditions and potential natural vegetation embodied by biome classifications. Therefore, we test a proxy for human factors in the form of land-cover and LUI, against a proxy for environmental factors, in the form of biomes, in their ability to predict SARs on a global scale.

## 2 Material and methods

### 2.1 Data

#### *Species Data*

We focused on terrestrial mammals due to their high endangerment status, 22% of mammals are currently threatened according to the IUCN (2013), and the availability of a recently updated global range maps (Schipper *et al.*, 2008; IUCN, 2013). We used extent-of-occurrence range maps provided by the IUCN (2013), which we overlaid with a grid to infer broad-scale species richness patterns. These range maps are currently considered the most comprehensive and detailed global dataset of mammal distributions (Di Marco & Santini, 2015). Range maps are expert-based maps of mammal distributions that depict the extent of occurrence, i.e. areas containing all known species occurrences. However, like all global spatially explicit datasets, errors and gaps occur. For example, species' areas of occupancy can be overestimated at fine spatial resolutions by including uninhabited areas (Jetz *et al.*, 2008). We therefore scaled the data to an equal area grid of approximately 110 km × 110 km or 1 degree at the equator as finer resolutions lead to high levels of false presences (Hurlbert & Jetz, 2007). We excluded all cells with <50% land area to minimize confounding effects of coastal areas, predominantly marine species, and small oceanic islands.

### ***Biome & Land-Use Data***

We used 14 biomes as defined by Olson and Dinerstein (1998, Figure III-1a). For land cover, we used 16 classes from the MODIS land cover map (Channan *et al.*, 2014, Figure III-1b). To assess LUI, we explored three categories of metrics related to the intensity of (a) inputs to agriculture, (b) outputs from agriculture, and (c) changes in system-level variables due to agriculture (Kuemmerle *et al.*, 2013). Input metrics relate to the intensity of land management along input dimensions, such as fertilizer use and irrigation. Output metrics describe the ratio of inputs and outputs, for example, yields (harvests/area). System-level metrics refer to the relationship between land management and properties of the socio-ecological system as a whole, such as the percentage of human appropriation of NPP (HANPP; Haberl *et al.*, 2007), and can provide a general idea of the overall management intensity.

As input metrics, we chose areas equipped for irrigation measured in percentage of each grid cell (Siebert *et al.*, 2005) and N-fertilizer application measured in percentage of each grid cell under fertilization (Potter *et al.*, 2010). Output metrics included cereal yields measured in t/ha/yr (Monfreda *et al.*, 2008). As system metric, we chose an integrated measure of land-use pressure on the environment, namely, human appropriation of NPP, which entered the analyses as percentage of each grid cell where any level of NPP is appropriated (Haberl *et al.*, 2007). The base cropland and land-cover maps used for the generation of the above datasets are given in the supplementary material Table SI III-1.

## **2.2 Statistical Analyses**

To construct SARs, we took 500 samples with replacement across our global grid. Samples were chosen randomly in terms of the total land area they covered, and ranged from a square window size of 1x1 to 15x15 grid cells. Samples were randomly placed and non-nested, i.e. one sample was not necessarily contained within the previous sample but entirely random in location, therefore some overlap could occur (resulting in a type IIB SAR curve, Scheiner, 2003).

Our models were based on the power law SAR, where  $S = c \cdot A^z$  relates species richness (S) to the area (A) of habitat, 'z' is the rate of change in species numbers, and 'c' is the taxon- and region-specific constant of per unit area species richness (Arrhenius, 1921). We systematically fitted different interactions to SARs that take into account the potential effects of land cover, biomes and each LUI metric, and compared their ability to predict large-scale species richness patterns. We tested two different model types. The first model fitted the

species-area relationship with area as the only predictor. The equation for this universal global model takes the form of:

$$(1) \quad \log_{10}(S) = \log_{10}(c) + z * \log_{10}(A)$$

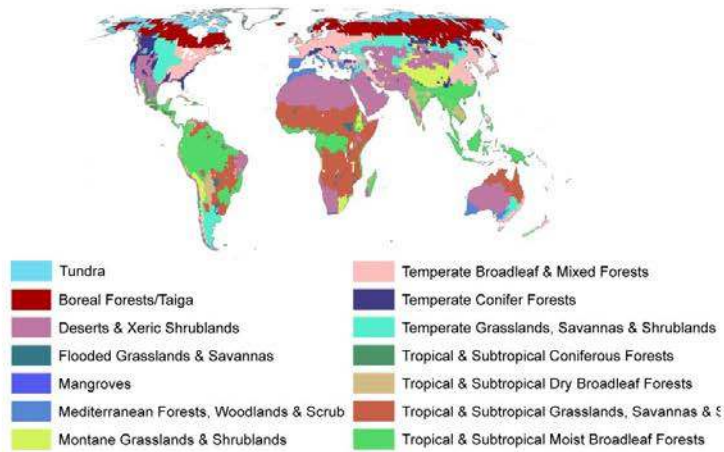
The second model included additional terms related to the percentage cover of either: biome, land cover or LUI, in each sampling unit. These were added as interaction effects to the area term in the model, as shown in equation 2:

$$(2) \quad \log_{10}(S) = \log_{10} c + \sum_{i=1}^n z_i \log_{10} A * R_i$$

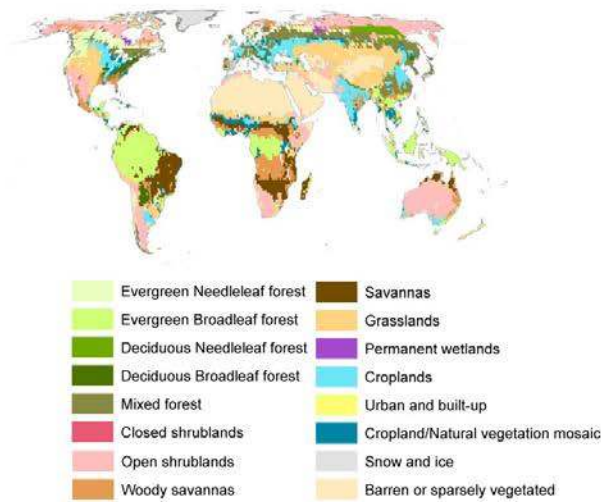
‘ $R_i$ ’ refers to the proportional area for each class  $n$  (i.e. biome class, land cover class, land-use intensity class, etc.). The biome model included 14 biomes and the land cover model included 16 land cover classes (excluding water). In order to generate SARs for the LUI models, we generated four classes – no LUI (where there was no agricultural activity), followed by high, medium, and low LUI (split by terciles, Figure III-1c). A separate model was run for each LUI metric resulting in a total of seven models - one universal global model, one biome model, one land cover model, and four LUI models.

To estimate the predictive power of each of the seven models, we applied a 10-fold cross-validation and calculated the squared correlation coefficient between predicted and observed values (following abbreviated with  $r^2$ ) (Harrell, 2001). During initial model development we found spatial autocorrelation in the residuals (from *Moran's I*), we therefore followed the approach taken by Gerstner *et al.* (2014) and employed simultaneous autoregressive models (Kissling & Carl, 2008) using the R 3.1.2 statistical analysis software (R Core Development Team, 2012), function *spautolm* in the package *spdep* (Bivand *et al.*, 2012). This method assumes spatial autocorrelation in a second error term which explicitly models spatial dependence in the residuals (Dormann, 2007) and is an established method for accounting for spatial autocorrelation in SAR samples (Kissling & Carl, 2008). We chose a neighbourhood structure based on the minimization of the residual spatial autocorrelation (Kissling & Carl, 2008; Gerstner *et al.*, 2014). We found an optimal neighbourhood distance of five grid cells (550 x 550 km). Due to the spatial structure of the data, parameter estimates were strongly influenced by the random spatial configuration of the 500 samples, i.e. sample location had a large effect on the  $r^2$ . We therefore re-ran our sampling approach 1,000 times (each run contained 500 different random sampling locations).

(a)



(b)



(c)

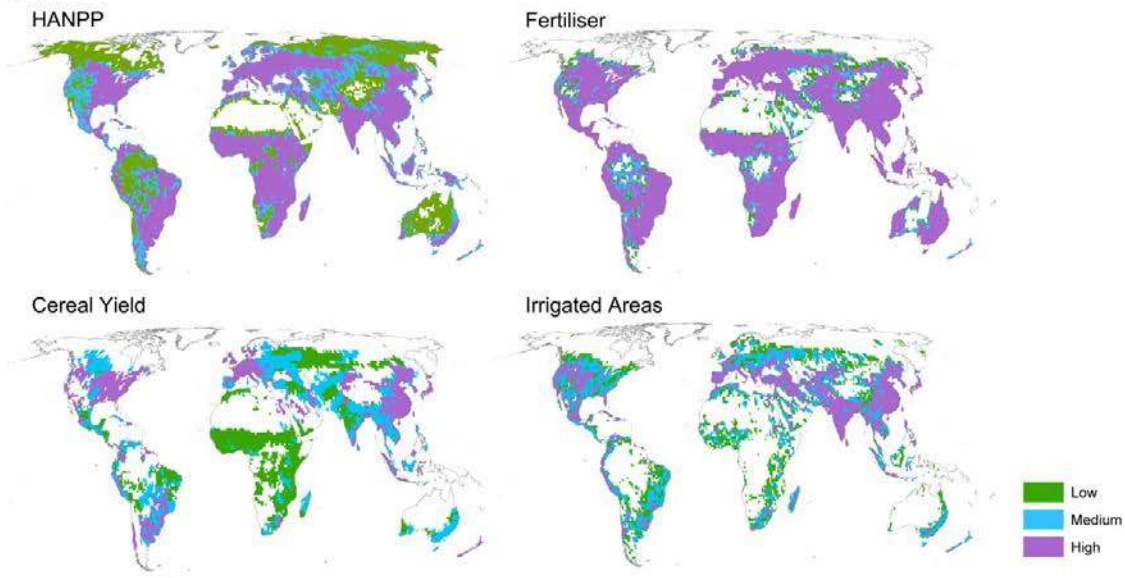


Figure III-1 Maps of potential factors causing variation of species–area relationships (SARs): (a) Biomes (Olson & Dinerstein, 1998), (b) Land Cover (Channan *et al.*, 2014) and (c) Land-Use Intensity (LUI) split into high (shown in purple), medium (blue), low (green) and no use (white) levels for the following datasets: human appropriation of net primary productivity (HANPP; Haberl *et al.*, 2007), fertiliser inputs (Potter *et al.*, 2010), cereal yield (Monfreda *et al.*, 2008) and areas equipped for irrigation (Siebert *et al.*, 2005). Due to many 100% values, areas of high intensity are larger than other areas. The maps are projected using Eckert IV projection.

Our final results reported here are thus based on the average parameter estimates of 1,000 sampling runs and associated model runs after trimming the most extreme 5% of model results. We tested linear, logarithmic and power models. In line with previous studies (Connor & McCoy, 1979; Dengler, 2009; Gerstner *et al.*, 2014; Matthews *et al.*, 2015), we report here only the power SAR (where area and species richness are log<sub>10</sub>-transformed prior to analysis), results for the linear and logarithmic models are reported only in the supplementary material (Table SI III-2).

### 3 Results

The inclusion of biomes, land cover or LUI all significantly improved the predictive ability of SARs compared to the universal global model (Table III-1). The biome model and the HANPP model had the best predictive power, both with a cross-validated  $r^2$  of 0.49 (compared to an  $r^2$  of 0.15 for the global model). The land cover model had the third highest  $r^2$  of 0.46 (Table III-1). Thus, modelling according to one global relationship would lead to large over- or underestimations of species richness, depending on the biophysical characteristics of the area of interest. We found a wide margin in the performance of LUI metrics – ranging from average  $r^2$  values of 0.49 to 0.26 (Table III-1), along with many different relationships with species richness in terms of high, medium and low LUI. HANPP, the only system metric investigated, out-performed all other LUI metrics (Table III-1).

Table III-1 Predictive ability of each simultaneous autoregressive model via 10-fold cross validation (results are averaged over 1000 model runs). The global model only included area as a predictor of species richness. Other models included either: Biomes (Olson & Dinerstein, 1998), Land Cover (Channan *et al.*, 2014) or Land-Use Intensity (LUI) split into high, medium, low and no-use levels for the following datasets: human appropriation of net primary productivity (HANPP; Haberl *et al.*, 2007), fertiliser inputs (Potter *et al.*, 2010), cereal yield (Monfreda *et al.*, 2008) and areas equipped for irrigation (Siebert *et al.*, 2005).

	Mean $r^2$	SD
LUI - HANPP	0.49	0.11
Biome	0.49	0.14
Land Cover	0.46	0.15
LUI - Fertiliser	0.44	0.13
LUI - Cereal Yield	0.31	0.13
LUI - Irrigation	0.26	0.12
Global	0.15	0.11

### 3.1 SARs by Biome

The addition of biomes to the global model increased its predictive power from  $r^2 = 0.15$  to  $r^2 = 0.49$ . Furthermore, SARs for individual biomes differed both in their intercept and  $z$ -values (Figure III-2). The boreal forest/taiga biome had the lowest  $z$ -value estimate (0.14), which indicates low levels of species increase in larger areas. The highest  $z$ -value and thus highest rate at which species richness increases with area was found in the tropical and subtropical coniferous forests biome ( $z = 0.49$ ).

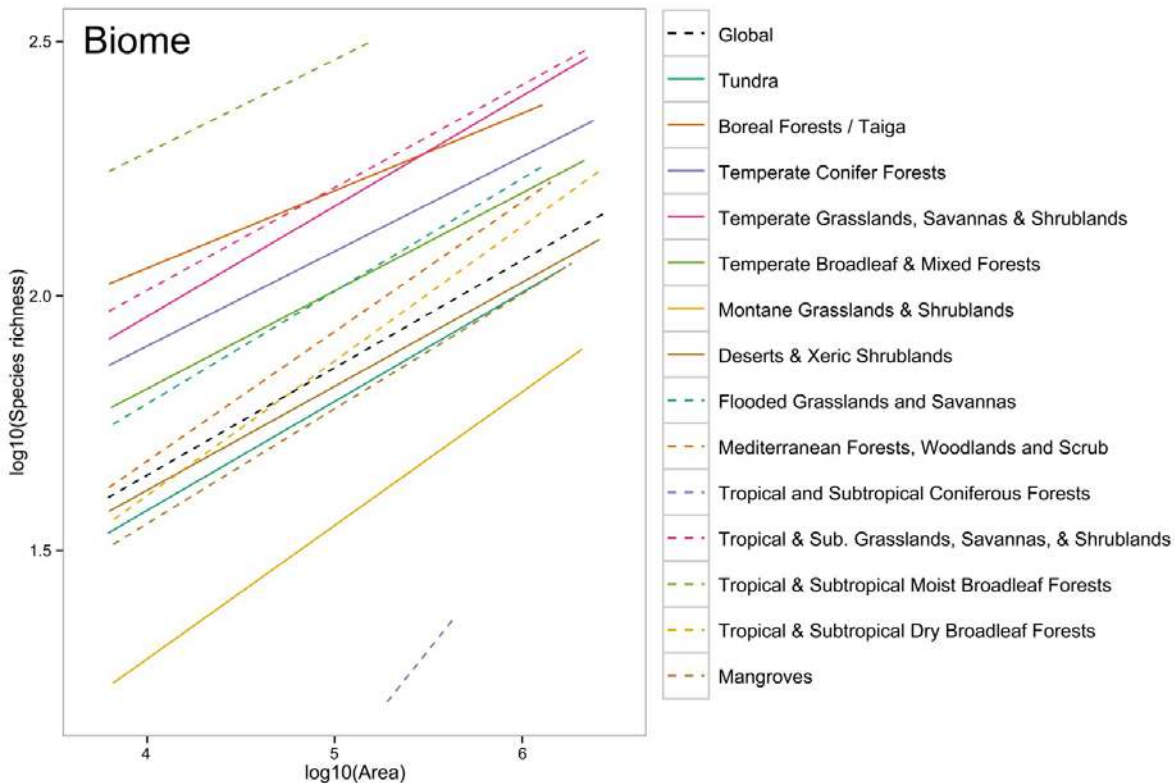


Figure III-2 Species-area relationships (SARs) in log-log space (area relates to  $\text{km}^2$ ) for biomes.

### 3.2 SARs by Land Cover

Land-cover specific SARs also increased the model  $r^2$  (0.46). As for biomes, we found a large range in SAR parameter estimates (Figure III-3, Table III-2). The highest  $z$ -value and thus the highest rate of species gain with increasing area was found for grasslands (0.31), snow and ice was found to have lowest  $z$ -values of 0.05. Results for land cover classes of less than 5% of the total area are not reported here as they tended towards extreme results due to their small area, and thus lack of samples, these comprise of closed shrublands, permanent wetlands and urban and built-up areas (Table SI III-3 for standard deviations, and 5% and 95% percentile values of estimates).

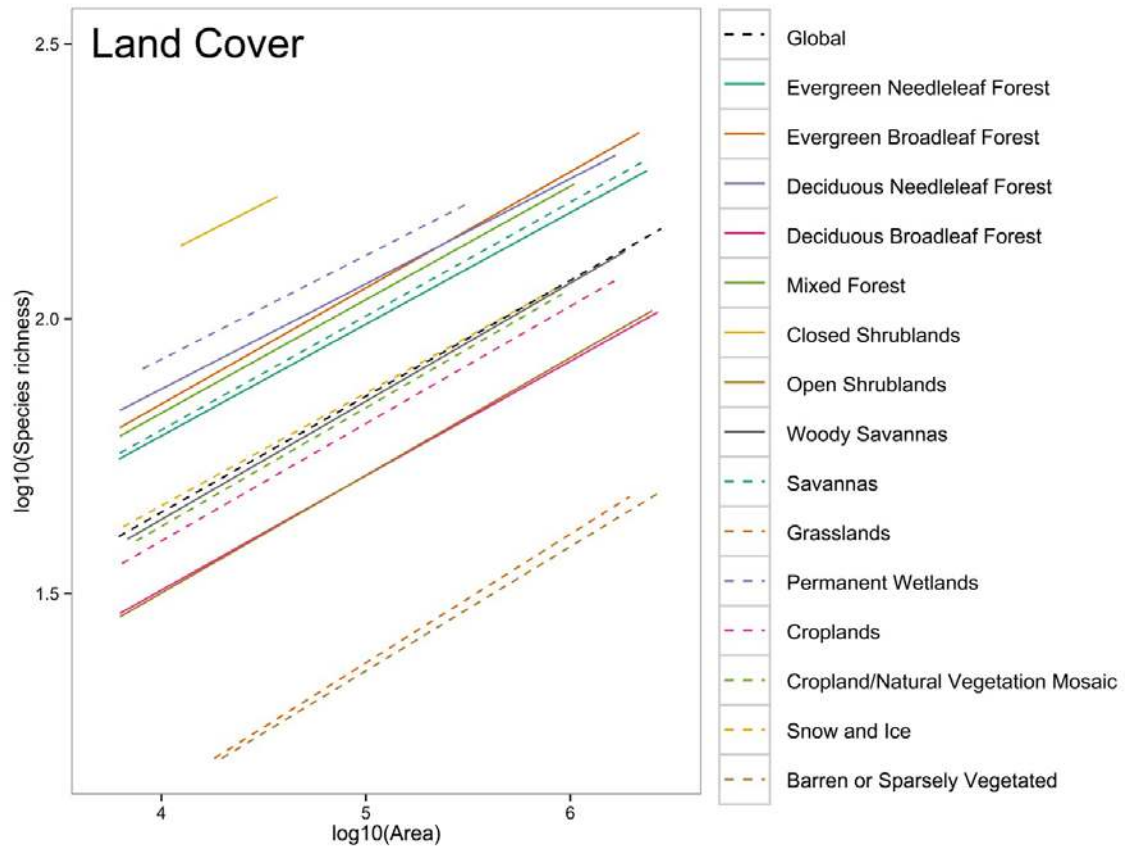


Figure III-3 Species-area relationships (SARs) in log-log space (area relates to km<sup>2</sup>) for land cover.

### 3.3 SARs by LUI

While all LUI metrics improved the predictive ability of the models from the global baseline, there was a wide margin in  $r^2$ , from the HANPP model with an  $r^2$  as high as that of biomes (0.49) to the irrigated areas model with an  $r^2$  of 0.26. Furthermore, the relationship between different levels of LUI and species richness was not constant across LUI metrics (Figure III-4, Table III-2). Compared to the biome and land-cover parameter estimates, a relatively low range in  $z$ -values and species richness predictions for LUI models was found. The highest species increase with area was found for medium levels of fertilizer application ( $z = 0.27$ ), the lowest species increase with area was found where there was no HANPP activity ( $z = 0.20$ ). In terms of the overall relationship of species richness and LUI, for the HANPP model, low intensity was associated with highest species richness, followed by high intensity and then medium levels associated with the lowest levels of species richness (Figure III-4, Table III-2).

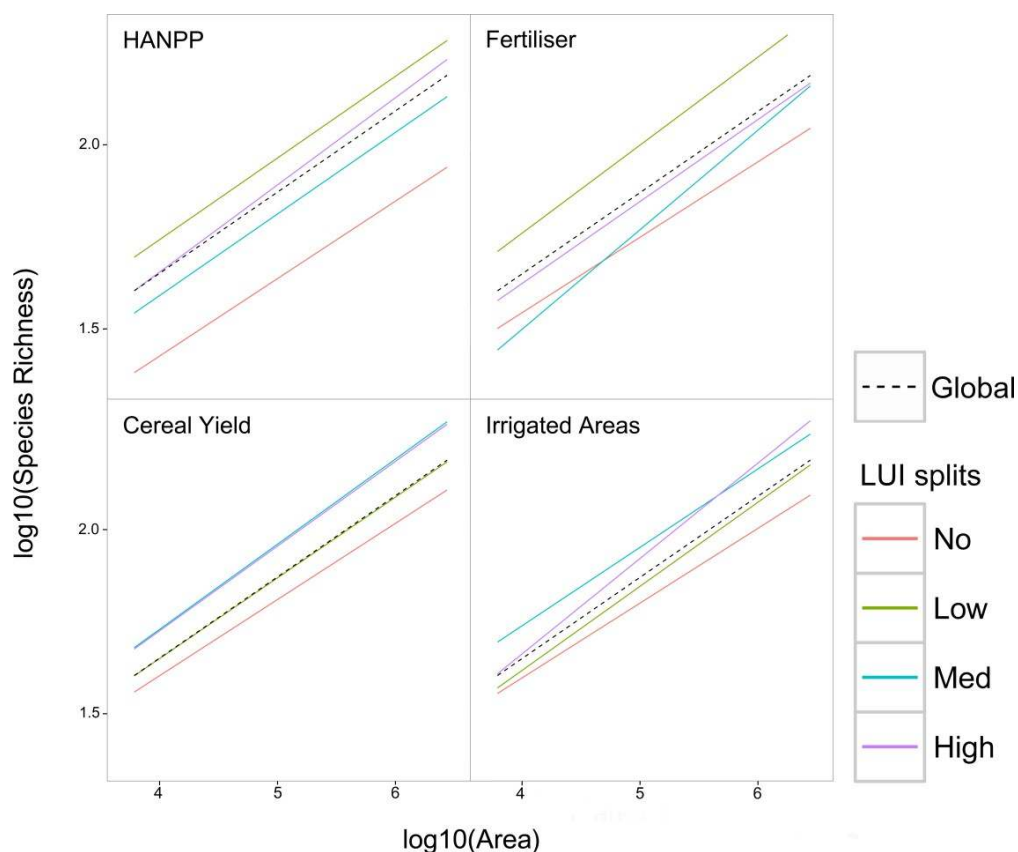


Figure III-4 Species-area relationships (SARs) in log-log space (area relates to km<sup>2</sup>) for land-use intensity (LUI), split into high, medium, low and no-use levels for the following datasets: human appropriation of net primary productivity (HANPP; Haberl *et al.*, 2007), fertiliser inputs (Potter *et al.*, 2010), cereal yield (Monfreda *et al.*, 2008) and areas equipped for irrigation (Siebert *et al.*, 2005).

Fertilizer application exhibited the same overall relationship as HANPP, but with one distinct difference – due to a higher z-value in the SAR for medium-intensity fertilizer application, in larger areas, medium- and high-intensity fertilizer application were associated with similar levels of species richness (Figure III-4, Table III-2). For cereal yields, medium- and high-intensity were associated with similarly high species richness regardless of area. Unlike HANPP and fertilizer application, higher species richness was associated with higher LUI for cereal yields and irrigated areas (Figure III-4). For all LUI metrics tested, species richness numbers were lowest in areas without any land use, which generally represent ice-covered and desert lands.



Table III-2 Parameter estimates for the species–area relationship (SAR): the slope  $z$  and intercept,  $\log_{10}(c)$ , of SARs in log–log space. Biome and land cover (LC) classes with less than 5% of the total land area are indicated with an \*

		$z$	Intercept
Global		0.22	0.75
Biome	Tundra	0.21	0.70
	Boreal Forests / Taiga	0.14	1.07
	Temperate Conifer Forests	0.20	0.88
	Temperate Grasslands, Savannas and Shrublands	0.20	0.91
	Temperate Broadleaf and Mixed Forests	0.20	0.83
	Montane Grasslands and Shrublands	0.27	0.42
	Deserts and Xeric Shrublands	0.21	0.71
	Flooded Grasslands and Savannas	0.23	0.76
	Mediterranean Forests, Woodlands and Scrub	0.26	0.65
	Trop. Subtrp. Coniferous Forests	0.49	0.00
	Trop. Subtrp. Grasslands, Savannas & Shrub.	0.21	0.90
	Trop. Subtrp. Moist Broadleaf Forests	0.17	1.12
	Trop. Subtrp. Dry Broadleaf Forests	0.26	0.60
	Mangroves*	0.23	0.65
LC	Evergreen Needleleaf forest	0.20	1.01
	Evergreen Broadleaf forest	0.22	1.04
	Deciduous Needleleaf forest	0.20	1.11
	Deciduous Broadleaf forest	0.29	0.72
	Mixed forest	0.20	1.04
	Closed shrublands*	0.27	1.29
	Open shrublands	0.23	0.75
	Woody savannas	0.24	0.85
	Savannas	0.21	1.01
	Grasslands	0.31	0.40
	Permanent wetlands*	0.20	1.15
	Croplands	0.23	0.83
	Urban and built-up*	0.18	0.37
	Cropland/Natural vegetation mosaic	0.24	0.84
	Snow and ice	0.05	0.97
Barren or sparsely vegetated	0.23	0.44	
HANPP (% use /grid)	No LUI (0)	0.20	0.59
	Low (0.6-91.3)	0.22	0.86
	Med (91.3-99.9)	0.22	0.72
	High (100)	0.23	0.72
Fert (% use)	No LUI (0)	0.21	0.73
	Low (2.9-40)	0.24	0.81

/grid)	Med (40-80)	0.27	0.41
	High (80-100)	0.23	0.73
Irr	No LUI (0)	0.21	0.78
(%/grid)	Low (0.01-0.2)	0.23	0.70
	Med (0.2-1.7)	0.21	0.88
	High (1.7-82)	0.26	0.63
Cereal	No LUI (0)	0.21	0.77
(t/ha/yr)	Low (0.2-1.6)	0.22	0.77
	Med (1.6-3.1)	0.23	0.80
	High (3.1-10.7)	0.23	0.81

### 3.4 Spatial arrangement of samples

Across all models, results varied substantially depending on the spatial location of the samples. When examining results from one single model run (with one sample set) we found that the model  $r^2$  ranged from a minimum of zero to a maximum of 0.87 (see Table SI III-4). Therefore, the random location and size of the samples alone, in extreme cases, could account for an  $r^2$  that explained nothing or close to all variation in species richness.

## 4 Discussion

The objective of this study was to assess whether SARs are improved by better representing the geographic variation of its parameters. We found that the addition of biomes, land-cover and land-use intensity (LUI) all improve global predictions of species richness. Furthermore, some land-cover and LUI metrics perform as well as biomes in predicting species richness.

In terms of LUI metrics, we found diverse interactions with SARs both in predictive ability and relationship between high, medium and low LUI and species richness. This adds evidence to research suggesting that metrics of LUI have distinct global patterns (Kehoe *et al.*, 2015) and relationships with biodiversity (Yamaguchi & Blumwald, 2005; Felton *et al.*, 2010; Alkemade *et al.*, 2012).

Finally, we found that HANPP, our only overall metric of LUI, was the best predictor of species richness when compared to other LUI metrics. This shows that broader LUI metrics can better predict SARs, likely due to their comprehensive nature. The predictive ability of HANPP may also provide support for the species-energy hypothesis, since net primary productivity can be seen as a form of available energy (Wright, 1990). The human

appropriation of high levels of energy in the form of net primary productivity may result in a loss of species richness at a landscape scale (Haberl *et al.*, 2014). We find that low HANPP levels are associated with higher species richness, however, high and medium HANPP levels are less intuitive – with species richness higher in areas of high HANPP. Our analysis was not causal but predictive, thus we cannot provide strong evidence with regard to the shape of the species-energy or species-HANPP relationship. Overall, we show that at a broad spatial grain, factors related to human activity are on a par with biophysical factors in predicting species richness.

#### 4.1 Geographic Variability in SARs

We found that including spatially explicit variables in species richness models improves predictions of global SARs. Furthermore, we found a signal between land use and species richness that is equally strong as that between species richness and biomes. Thus, despite most research focusing on a local grain size when addressing the relationship between land use and species richness (see Newbold *et al.*, 2015 for review), and global studies with larger grains generally focusing on natural biophysical drivers (Hawkins *et al.*, 2003b; Hawkins *et al.*, 2003a; Field *et al.*, 2009; Hortal *et al.*, 2012), we show that human factors may play a more dominant role in predicting global biodiversity patterns than previously thought.

Our analyses do not provide a causal link of land use and biodiversity patterns. This link has been shown at local scales, where land use in the form of conversion from natural habitat and intensification of existing agricultural land results, on average, in decreased species richness (Newbold *et al.*, 2015). Our results are the first to show how impacts may aggregate to affect species richness patterns at the global scale, which is important considering the acceleration of land-use change in recent times, and its importance in driving both current and future biodiversity loss (Sala *et al.*, 2000; Pereira *et al.*, 2012). However, land use itself depends on climate, soils, and productivity. Many of these same factors are the basis on which biomes are delineated, where species richness patterns are also closely related to climate and productivity variables (Hawkins *et al.*, 2003a). Thus, attribution as to which factors are driving species richness patterns (land use vs. environmental factors) is challenging based on broad-scale analyses.

When compared with results from previous research, our biome model parameters performed similarly to those found by Gerstner *et al.* (2014) for plant species richness. In both our results and those of Gerstner *et al.* (2014), the boreal forest/taiga biome had the lowest  $z$  estimate (0.14 and 0.08 respectively). Furthermore, the biome with the largest  $z$

estimate was the tropical and subtropical coniferous forests biome (0.49 and 0.45). This indicates that there is a high concordance of biome explicit SARs for plants and mammals on a global scale.

Regarding the predictive ability of the models, the main difference in results is that Gerstner *et al.* (2014) found that land cover had a relatively lower  $r^2$  when compared to our land cover result. This may be due to five reasons. First, the biodiversity datasets for plants used by Gerstner *et al.* (2014) were only available for a set number of locations, thus producing limitations in global predictions. Second, the plant dataset used by Gerstner *et al.* (2014) was not as up to date as the mammal data (IUCN, 2013) used here. Third, plants and mammals have different responses to land-use and LUI (Gibson *et al.*, 2011). Fourth, our study uses a different land cover map from 2014, not available at the time of Gerstner's study. Finally, both studies are global in extent and at this scale species extinctions are relatively rare, where local extinctions and range contractions are more common, such processes are often not reflected at our coarse spatial grain.

## 4.2 Diversity of LUI metrics

Understanding the relationship between LUI and biodiversity is important since LUI is set to further accelerate in the future as 'sustainable intensification' gains support (Foley *et al.*, 2011). Previous studies focusing on small grain sizes have found that a higher proportion of agricultural land and higher LUI can have negative effects on biodiversity (Martins *et al.*, 2014; Newbold *et al.*, 2015). However, due to the diverse patterns of LUI metrics globally and their likely diverse effects on biodiversity, we expected that LUI metrics would have a variety of relationships with species richness. Our results suggest that this is the case and that LUI metrics have varied relationships with species richness - at least for a 1 degree grain size.

In terms of model performance, LUI metrics exhibited diverse predictive abilities in relation to SARs, ranging from 49% (HANPP) to 26% (areas equipped for irrigation). This again illustrates the non-uniformity in LUI metrics, not just in their spatial patterns but also in their ability to predict global patterns of species richness. Of LUI metrics, HANPP had the best predictive ability. This is likely because this metric covers a wider variety of potential agricultural land uses, namely, wherever any form of activity related to appropriating NPP is present. It is thus logical that the LUI metrics that cover a broader spectrum of human land use will naturally have the best predictive ability.

We show that there is a large diversity in the relationship between high, medium and low LUI, and species richness, however, our research is of coarse spatial grain, with relatively large distributions in parameter estimates (Table III-2). We thus cannot provide the answers as to which forms of LUI and at what level may be most detrimental to biodiversity. For this, experimental and observational small-scale research and synthesis are needed. However, we do show that there is a large diversity in the relationship between LUI and species richness and that the global story is not as one dimensional as fine-scale studies often suggest, i.e. higher LUI results in lower species richness.

### **4.3 Importance of the spatial location of samples**

We found that our modelling results were highly dependent on the spatial location and size of samples (see Table SI III-4), while we controlled for this by running 1,000 models and taking the average of the parameter estimates, many studies do not have this option and must work with the limited samples that are available. Our results have implications for studies which use incomplete datasets and often draw broad conclusions. Where studies are not as fortunate to have a complete global dataset, caution should be taken in model results and their probable high reliance on sample size and spatial location.

### **4.4 Limitations**

The goal of this study was to assess whether or not the consideration of human influence in the form of land cover and LUI can improve predictions of SARs and if so, if it is comparable to that of environmental measures. Thus, we did not control for other factors at play in driving patterns of species richness, and models that include one LUI metric do not account for the many other potential land-use activities and environmental factors at play on the same landscape. Nor did we account for the collinearity inherent in our datasets where species richness, biomes, and agricultural suitability are closely tied to climate and topography. Furthermore, we do not know many species' tolerances to land-use change and even in the cases where tolerances to land-use are known, extent-of-occurrence range maps usually do not reflect such changes. In the knowledge that the SAR is affected by grain size, where different patterns emerge at different spatial grains, (Turner & Tjørve, 2005), we chose 110 x110 km grid cells as it is the minimum acceptable grain (Hurlbert & Jetz, 2007). It is therefore expected that the relationships we found are scale-dependent and should not be extrapolated. Together, these issues present a challenge inherent in implying any form of causality between our predictor variables and our biodiversity distributions.

We compiled a set of land cover and LUI metrics with the highest quality currently available. Nevertheless, despite considerable recent progress, numerous gaps exist regarding the availability of alternative indicators and the difficulties in their measurement related to issues with data availability, accuracy and error propagation (Kuemmerle *et al.*, 2013). Uncertainties in the accuracy of current LUI maps are often high due to inconsistent input data and limitations with processing algorithms and positional accuracy. Furthermore, there is a lack of formal validation for many of these datasets (Verburg *et al.*, 2011). Systematically collected ground-based data only cover a few regions of the globe, statistical data are often only available at the national scale, and remote sensing cannot easily capture the subtle spectral effects of LUI changes (Kuemmerle *et al.*, 2013). Furthermore, the fertilizer (Potter *et al.*, 2010) and cereal yield (Monfreda *et al.*, 2008) LUI maps used here all rely on one cropland map (Ramankutty *et al.*, 2008), and inaccuracies in the base map can therefore propagate (see Table SI III-1).

## 5 Conclusions

Human land use has been shown to drive biodiversity loss at the local scale, however, its ability to predict variation in global SARs had not previously been assessed. This study adds evidence suggesting that human land use may be an important predictor of species richness. Great attention has previously been paid to the past and present biophysical attributes at play in predicting patterns of species richness. Our findings suggest that human activity can better predict large-scale patterns of species richness than previously thought. This is useful information given that land use is the most important driver of local biodiversity patterns, and that land-use change is expected to accelerate in the future, as human population and per-capita consumption soar. In order to better predict and understand biodiversity patterns using SARs, we need to adopt a more nuanced view, with both land-cover and the intensity of land-use taken as potentially important factors in explaining variation in global species richness.

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## Supplementary Information

Table SI III-1 Input land cover and land-use intensity datasets

<i>Dataset</i> (citation, original scale, year)	<i>Description</i> (data value, reference year)	<i>Data Source</i>
<b>MODIS Land Cover</b> (Channan et al., 2014, 0.5° , 2014)	(% per grid cell, 2001- 2012)	Global Mosaics of the standard MODIS land cover type data product (MCD12Q1) in the IGBP Land Cover Type Classification. <a href="http://landcover.org/data/lc/index.shtml">http://landcover.org/data/lc/index.shtml</a>
<b>Land equipped for irrigation</b> (Siebert et al., 2005, 5min, 2000)	(% per grid cell, ~2000)	FAO, World Bank and other international organizations, <a href="#">USGC-GLCC-2.0</a> and <a href="#">JRC- GLC2000</a> land cover datasets used when no other spatial info available.
<b>Industrial and manure fertilizer application rates</b> (N, P) (Potter et al., 2010, 10km, 2000).	Nitrogen fertilizer nutrients applied to croplands (kg/ha, 1994- 2001).	FAO “Fertilizer Use by Crop 2002” combined with harvested area for 175 crops (Monfreda et al. 2008).
<b>Cereal Yield</b> (Monfreda et al., 2008, 5min, 2000)	Yields of 175 crops in (t/ha, 2000).	Census statistics & global cropland area (Ramankutty et al. 2008)
<b>HANPP</b> (Haberl et al., 2007, 5 min, 2000)	Human Appropriated Net Primary Productivity (per cent of NPP0, 2000)	FAO and Lund–Potsdam–Jena (LPJ) DGVM (18, 19) global vegetation models



Table SI III-2 10 fold cross validation for the power, log and linear global models.

Global Power	$\log(S) = \log(c) + z * \log(A)$	0.15
Global Log	$S = c + z * \log(A)$	0.13
Global Linear	$S = c + z * A$	0.15

Table SI III-3 Mean z and intercept (I) standard error, standard deviation, 5th and 95th percentiles of parameter estimates. Biome and land cover classes with less than 0.05% of the total land area are indicated with an \*.

		Z	Z(S D)	Z(Q5)	Z(Q95)	Intrep t	I(SD )	I(Q5)	I(Q95)
Biom									
e	Tundra	0.21	0.06	0.10	1.20	0.70	0.28	-0.27	4.14
	Boreal Forests / Taiga	0.14	0.04	0.08	2.08	1.07	0.19	-0.08	5.66
	Temperate Conifer Forests	0.20	0.06	0.08	83.93	0.88	0.28	-0.20	7.47
	Temperate Grasslands, Savannas and Shrublands	0.20	0.08	0.10	3.08	0.91	0.36	-1.16	4.87
	Temperate Broadleaf and Mixed Forests	0.20	0.05	0.08	64.50	0.83	0.22	0.20	33.37
	Montane Grasslands and Shrublands	0.27	0.10	-0.17	2094.16	0.42	0.54	-0.92	89.03
	Deserts and Xeric Shrublands	0.21	0.05	-0.01	46.20	0.71	0.26	0.23	7.07
	Flooded Grasslands and Savannas	0.23	0.14	-0.32	2217.68	0.76	0.73	-1.74	442.52
	Mediterranean Forests, Woodlands and Scrub	0.26	0.09	0.06	2.70	0.65	0.41	-0.54	8.64
	Trop. Subtrop. Coniferous Forests	0.49	0.59	-0.33	2217.68	-0.34	3.06	15.85	442.20
	Trop. Subtrop. Grasslands, Savannas & Shrub.	0.21	0.05	-0.02	60.94	0.90	0.23	0.47	281.85
	Trop. Subtrop. Moist Broadleaf Forests	0.17	0.05	0.11	1.87	1.12	0.21	-0.06	3.53
	Trop. Subtrop. Dry Broadleaf Forests	0.26	0.11	0.11	188.89	0.60	0.59	-2.63	99.10
	Mangroves *	0.23	0.13	-0.34	2217.68	0.65	0.60	-1.07	442.20

LC	Evergreen forest	Needleleaf	0.20	0.11	0.07	1.12	1.01	0.42	-0.48	10.08
	Evergreen forest	Broadleaf	0.22	0.14	0.10	8.11	1.04	0.46	-1.59	3.91
	Deciduous forest	Needleleaf	0.20	0.11	0.06	1.12	1.11	0.51	-0.51	2.82
	Deciduous forest	Broadleaf	0.29	0.19	0.03	1.99	0.72	0.99	-2.86	10.72
	Mixed forest		0.20	0.11	0.10	2.00	1.04	0.36	-0.53	3.36
	Closed shrublands *		0.27	0.55	-0.27	37.72	1.29	2.90	28.48	12.46
	Open shrublands		0.23	0.09	0.13	0.77	0.75	0.29	-0.47	2.81
	Woody savannas		0.24	0.09	0.13	1.49	0.85	0.30	-0.36	34.24
	Savannas		0.21	0.11	0.11	24.65	1.01	0.37	-0.60	15.81
	Grasslands		0.31	0.20	0.15	4.04	0.40	0.63	-4.32	1.73
	Permanent wetlands*		0.20	0.16	-0.22	1.38	1.15	0.70	-0.72	4.34
	Croplands		0.23	0.10	0.13	3.31	0.83	0.33	-0.49	8.09
	Urban and built-up*		0.18	0.19	-0.27	1.43	0.37	1.61	-6.37	288.82
	Cropland/Natural vegetation mosaic		0.24	0.12	0.12	100.46	0.84	0.43	-0.69	5.12
	Snow and ice		0.05	0.42	-1.80	1.57	0.97	1.38	-1.03	164.42
Barren or sparsely vegetated		0.23	0.15	-0.66	37.46	0.44	0.43	-0.32	23.71	
HAN										
PP	No LUI (0)		0.20	0.20	-0.27	2.90	0.59	0.95	-0.36	9.23
	Low (0.01-0.6)		0.22	0.11	0.12	1.77	0.86	0.40	-0.21	4.47
	Med (0.6-91.3)		0.22	0.11	0.12	1.75	0.72	0.61	-0.83	2.41
	High (100)		0.23	0.10	0.13	1.75	0.72	0.40	-0.06	3.28
Fert.	No LUI (0)		0.21	0.12	0.10	13.46	0.73	0.44	-0.05	4.00
	Low (0.01-40)		0.24	0.12	0.13	68.53	0.81	0.36	-0.10	2.01
	Med (40-80)		0.27	0.29	0.04	184.38	0.41	1.23	-0.89	123.96
	High (80-100)		0.23	0.35	0.00	24.53	0.73	1.89	-1.01	7.66
Irrigat										
.	No LUI (0)		0.21	0.09	0.11	2.66	0.78	0.34	0.13	2.82
	Low (0.01-0.2)		0.23	0.09	0.13	2.31	0.70	0.42	-0.28	2.22
	Med (0.2-1.7)		0.21	0.11	0.10	4.46	0.88	0.35	0.30	6.23
	High (1.7-82)		0.26	0.18	0.14	3.50	0.63	0.94	-1.67	5.24
Cerea										
l	No LUI (0)		0.21	0.09	0.12	1.60	0.77	0.36	-0.03	2.66
	Low (0.01-1.6)		0.22	0.12	0.12	1.95	0.77	0.58	-0.41	3.25

Med (1.6-3.1)	0.23	0.12	0.13	2.72	0.80	0.50	0.13	6.60
High (3.1-10.7)	0.23	0.11	0.13	1.68	0.81	0.41	0.05	4.55

Table SI III-4 Differences in  $r^2$  in order to test the effect of the spatial arrangement of samples from 1000 model runs each consisting of 500 sets of random samples.  $r^2$  min-max' refers to the most extreme model results from 1000 model runs. ' $r^2$  mean' is the mean result from 1000 model runs

	$r^2$ mean	$r^2$ min-max
LUI - HANPP	0.49	0.00-0.81
Biome	0.49	0.00-0.87
Land Cover	0.46	0.00-0.85
LUI - Fertiliser	0.44	0.00-0.83
LUI - Cereal	0.31	0.00-0.77
LUI - Irrigation	0.26	0.00-0.70
Global	0.15	0.00-0.61



**Chapter IV:**  
**Nature at risk: Modelling global biodiversity  
loss due to pathways of agricultural expansion  
and intensification**  
*(in review)*

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## **Abstract**

Agricultural land-use change is currently a leading cause of biodiversity loss, but few studies have explored what future land-use change may mean for biodiversity. Of these, the majority have focussed on assessing land-use effects in a few, highly constrained, path dependent, socio-economic, development scenarios. Here, we instead explore the full biophysical option space of how future agricultural change may affect biodiversity, using a simple and transparent approach. Specifically, we identify areas most at risk under two contrasting agricultural development pathways: expansion into suitable land and intensification of existing cropland. We then assess how these pathways affect local vertebrate species richness and abundance. We find particularly high risk of biodiversity loss due to agricultural expansion across the Amazon and Sub-Saharan Africa. Intensification risk-areas were mainly in India, Eastern Europe, and the Afromontane and African Great lakes region. The most at risk area of vertebrate species loss was in the Peruvian Amazon, where a combination of expansion and intensification would result in approximately 317 species lost in a 110 km grid cell. Many of our at risk regions were not adequately covered by conservation prioritization schemes or protected areas. On a national-level, Sub-Saharan African and Latin American countries dominated the top ten ranks of potential biodiversity loss. Suriname had the highest potential species richness loss followed by French Guiana and Guyana (219, 206, and 182 species lost on average per 110 km grid cell respectively). The DRC and Rep. of Congo both had the highest average loss in wildlife abundance (25%) followed by Suriname and Liberia (24%). In light of rising agricultural demand, our results highlight areas where future land-use change has the potential to affect biodiversity drastically, predominantly in the Amazon and Sub-Saharan Africa, and thus where effective land-use planning could proactively mitigate future land-use conflicts.

## 1 Introduction

Agricultural land-use change is a major driver of global biodiversity loss (Balmford *et al.*, 2012). Agriculture is in constant flux, characterized by expansion, intensification and abandonment, and these processes in turn shape biodiversity patterns predominantly through the loss of critical wildlife habitat, the introduction of non-native species, nutrient runoff, pesticide poisoning, increased greenhouse gas emissions, sedimentation of waterways, and changes in the biogeochemistry cycle resulting in water and soil degradation (Fahrig, 2003; Foley *et al.*, 2005; CBD, 2010). With the exception of abandonment, these processes generally have a negative effect on biodiversity. Furthermore, the effects of agriculture are not isolated but can extend to broader scales beyond the boundaries of field and pasture, due to factors such as pesticide and fertilizer runoff (Foley *et al.*, 2005; Lambin & Meyfroidt, 2011). With more than 38% of the world's terrestrial surface transformed to croplands and pastures, the detrimental effects of agriculture on biodiversity have undoubtedly reached global scales (Ramankutty *et al.*, 2008).

Despite the well-documented local impacts of agricultural land use on biodiversity (Dornelas *et al.*, 2014; Newbold *et al.*, 2015), factors, such as temperature, productivity, precipitation, energy, are generally considered dominant in driving species richness patterns at broad geographic scales (Hawkins *et al.*, 2003b; Belmaker & Jetz, 2015). However, recent work suggests that agriculture is an equally strong predictor of species richness as environmental factors at broad scales (Kehoe *et al.*, 2016) and that human pressures can predict range size better than biological traits (Di Marco & Santini, 2015). Unfortunately, the current generation of global-scale species range maps and land-use datasets have insufficient spatial and temporal resolution to establish more than correlative relationships between agriculture and biodiversity impacts. Yet a better understanding of how agriculture may affect biodiversity patterns is becoming increasingly important, as agriculture will both expand and intensify further in the coming decades in response to rapidly growing human demands for food, fuel, and fiber, which are expected to nearly double by 2050 (Tilman *et al.*, 2011). In response to this, agricultural land-use change is expected to remain the primary driver of terrestrial biodiversity loss in 2100 (Sala *et al.*, 2000).

Despite this, relatively few studies have assessed potential impacts of future agricultural land-use change on biodiversity, with the bulk of the global change literature on future biodiversity threats focussing on direct impacts of climate change (Titeux *et al.*, 2016). Furthermore, of the few studies that have assessed agricultural impacts, the majority have

focused on future impacts of a few agricultural scenarios using integrated assessment models (IAMs), particularly the GLOBIO and IMAGE projections (Sala *et al.*, 2000; Visconti *et al.*, 2011; de Baan *et al.*, 2013; Bellard *et al.*, 2014; Rondinini & Visconti, 2015; Visconti *et al.*, 2015). Such models can consider a wide range of societal (e.g., population growth, diet changes), economic (e.g., sector-specific changes, trade patterns), and institutional (e.g., policies) factors (Alkemade *et al.*, 2010), and are valuable in deriving multi-targeted development pathways and assessing the possible impact of specific policies (Müller & Lotze-Campen, 2012). However, while a central strength of IAMs are their complexity, this also comes at the cost of often large uncertainties related to the many parameters, sub-models, and input datasets that IAMs require, and thus also high uncertainty associated with the outcomes of these models, including the spatial configurations of future land systems (Rosen, 2015). The details of how IAM results are derived are often not described transparently, making reliability, reproducibility, and validation challenging (Rosen, 2015). Moreover, while IAM are potentially powerful in predicting the impacts of gradually changing drivers (e.g., population growth, diet changes, climate change), they are weak in capturing the effects of sudden and unforeseeable changes in drivers of land-use change, such as revolutions, technological breakthroughs, or economic crisis, despite such shock events frequently occurring and having a strong impact (Müller *et al.*, 2014; Jepsen *et al.*, 2015; Ramankutty & Coomes, 2016). Approaches that are simple, more direct, and transparent, and that enable the exploration of the full option space of possible future development pathways are thus needed and complimentary to IAM approaches (Erb *et al.*, 2016a).

Very few studies have used such an alternative approach on a global scale. One of the most prominent is a study by Phalan *et al.* (2014) that spatially prioritised by favouring either low intensity expansion (land sharing) or closing yield gaps (land sparing) according to what is least harmful to biodiversity. This approach identified regions where increasing crop yields could pose the greatest risks to the conservation status of birds. However, limited spatial data on the land-use effects of biodiversity was available at the time of this study. Another major study focused on mapping the potential for expansion, intensification, or both, in terms of changes in yield gaps (Shackelford *et al.*, 2015). Regions of potential conservation conflict calculated as the concordance of non-cropland in a 2km radius of cropland and yield gaps, alongside threatened species were highlighted. However, areas not suitable for cropland were not excluded from the analysis, and data to explicitly assess biodiversity loss was not



available (Shackelford *et al.*, 2015). Moreover, both studies' focus on yield gaps alone, which may miss crucial land-use intensity impacts on biodiversity (Kehoe *et al.*, 2015).

All in all, gaining a broader perspective by considering alternative methodologies in estimating the effects of future agricultural development on biodiversity is crucial. Assessing the spatially explicit biodiversity impact of pathways of expansion and intensification is a fundamental first step in this regard. This requires translating agriculture's known local biodiversity impacts into a more causal understanding of agriculture's ecological impacts that can be applied to assess the local biodiversity effects across broad geographic extents. Recently available datasets and methods have made better estimates of agricultural impacts on biodiversity possible. Using over 1 million data points available from the PREDICTs database (Hudson *et al.*, 2014), Newbold *et al.* (2015) modeled the local effects of various types of land use at various levels of intensity on biodiversity. These relationships were used to obtain spatially explicit, global estimates of historical and projected future changes in species richness, rarefied richness, and abundance due to land use (Newbold *et al.*, 2015).

Given that these models factor in multiple forms of land-use intensity, they provide a ready means for isolating and assessing the potential future impacts of different agricultural development pathways on extant biodiversity. Here we capitalize on these models to assess the potential net change in biodiversity due to two main agricultural development pathways of agricultural intensification and expansion. Our pathways here do not attempt to serve as predictive scenarios connected to certain trends regarding human population, consumption, or technology, and are not direct comparisons in terms of agricultural output. Instead, we consider the dominant processes of agricultural land-use change, and thus allow for exploring the potential full effect of different modes of biophysically possible agricultural change from fine spatial grain (1 km<sup>2</sup>) to national level. Our goal was to answer the following three research questions: (1) How may alternative future agricultural development pathways of agricultural expansion and intensification shape global species richness and abundance? (2) Do protected areas and conservation prioritization schemes align with our high risk areas? (3) What countries are most at risk in terms of biodiversity loss, conservation spending, and agricultural growth?

## 2 Methods

### 2.1 Land-use data

We used a land-systems-based approach, and developed possible agricultural development pathways in terms of shifts between land systems (e.g. from low-intensity to high-intensity cropland). Land systems represent the interface between the majority of human activities and the natural environment and consist of hierarchical categorical classifications that combine metrics of land cover, land-use intensity and livestock density (van Asselen & Verburg, 2012).

We first developed an updated global land systems map to utilize the most recent land-cover and land-use datasets available and in order to work at a finer spatial resolution than previously possible (from an original resolution of  $\sim 9.25 \text{ km}^2$  to  $\sim 1 \text{ km}^2$ , Figure SI IV-1). We achieved this by following the decision tree classification (Figure SI IV-2 taken from (van Asselen & Verburg, 2012) to map land systems globally while using updated datasets. We compiled six datasets related to cropland extent (Fritz *et al.*, 2015), tree cover (Hansen *et al.*, 2013), urban and bare areas (ESA-CCI, 2016), livestock density (Wint & Robinson, 2007), and yield gaps (IIASA/FAO, 2012; see Table S1 for full details on datasets).

To investigate biodiversity loss due to potential agricultural expansion, we included a biophysical land suitability condition to the natural classes. This classification delineated natural areas that are ‘very high’ to ‘marginally’ suitable for cropland (Fischer *et al.*, 2012). We included areas suitable for high-input level cropland (in terms of optimum applications of nutrients and chemical pest, disease and weed control) rather than only low-input areas (characterized by labor intensive techniques, no application of nutrients, no use of chemicals for pest and disease control) in order to avoid being overly conservative in terms of where cropland is possible. In saying this, the difference in spatial extent between high and low input level areas suitable for cropland was minor (Fischer *et al.*, 2012). Land inside protected areas was not excluded from the analysis for two main reasons. First, protected areas are human controlled land-cover classes, are thus susceptible to change, and may not be protected in the future (Mascia & Pailler, 2011). Second, to explore whether current protected areas are located in areas with a high risk of biodiversity loss due to our potential agricultural development pathways.

## 2.2 Agricultural development pathways

We developed three possible pathways of future agricultural land-use change: (1) expansion, (2) intensification, and (3) a combination of both intensification and expansion. Our pathways do not compare across production targets, and therefore do not speak to whether one pathway is preferable over another in terms biodiversity loss. We instead identify areas at risk in terms of the biophysical option-space related to expansion, intensification, or a combination of both. This is worthwhile since both expansion and intensification are likely to continue in the future, and it is therefore crucial to know where biodiversity could be most affected by which specific agricultural development pathway.

Our expansion pathway does not intensify current cropland, but extends low-intensity cropland systems into natural areas deemed suitable for cropland (Fischer *et al.*, 2012). This pathway represents continued loss of natural ecosystems due to the lack of yield gains on existing land systems stemming from inadequate resources or capital, or available inexpensive land for expansion, as is currently apparent in many tropical deforestation frontiers of South America, Sub-Saharan Africa, and South-East Asia (Gibbs *et al.*, 2010; Mueller *et al.*, 2012).

On the other hand, our intensification pathway consisted of all land-systems currently under any form of agricultural activity transforming to the highest level of cropland intensity for that class without any expansion into natural areas. For example, an area classified as *extensive* (low intensity) cropland would become *intensive* cropland (Table IV-1). This pathway represents a global push to close yield gaps in less developed regions, as is currently happening across much of Europe, the United States, or parts of South America (Mueller *et al.*, 2012). Many crop yields are heavily dependent on fertilizer use and irrigation, with substantial production increases (45% to 70% for most crops) possible if yield gaps were closed (Mueller *et al.*, 2012). North and West European countries are already close to their maximum attainable yield, with North America, South-East Asia, and Oceania achieving more than 60% of their potential production. However, Africa and Eastern Europe are currently producing only 40% of their potential (Pradhan *et al.*, 2015). In our intensification pathway, closing such yield gaps would be achieved by moving from low-intensity farms with little to no fertiliser, pesticide, irrigation or mechanisation to highly-intensified, conventional monocultures that are characterised by high inputs and large fields (in line with the classification system of Hudson *et al.*, 2014).

Finally, the third pathway is a combination of both expansion and intensification, where cropland expands into natural areas wherever possible and intensification takes place in all agricultural areas (both long-standing and newly converted). This represents the pathway of most drastic change, where both processes of intensification and expansion increase unabated in response to rising demand, current trends in parts of Argentina, Paraguay, or Brazil reflect this (Angelsen & Kaimowitz, 2001; Nepstad & Stickler, 2008). This pathway also accounts for Jevon’s paradox, where yield improvements spur further expansion due to better opportunities for farming, and is a likely pathway for some regions of Sub-Saharan Africa (Hertel *et al.*, 2014).

Table IV-1: Three pathways of land-use change: (i) expansion of low-intensity (extensive) cropland into uncultivated areas, (ii) intensification of existing cropland, and (iii) a combination of both, where existing cropland and newly converted regions are intensified.

<b>Original Land System</b>	<b>Expansion</b>	<b>Intensification</b>	<b>Both</b>
Forest and Grassland	Converted to Extensive Cropland	No Change	Converted to Intensive Cropland
Extensive to Medium Intensity Cropland	No Change	Intensified	Intensified
Intensive Cropland	No Change	No Change	No Change

Our pathways did not include changes in livestock density on pastures. For example, if a system was *extensive* cropland with few livestock, in the intensification pathway, it would become *intensive* cropland with few livestock (Table SI IV-2). This decision was based on the assumption that intensified livestock management will join the ‘livestock revolution’ – a shift away from pasture-based management towards industrialised feedlots that depend on crop-based feeds rather than local land resources. This process is already underway in many rapidly growing economies of Asia and South America (Delgado *et al.*, 2001; Naylor *et al.*, 2005).

### 2.3 Biodiversity data

We calculated total species richness by overlaying extent of occurrence maps for birds (BirdLife & NatureServe, 2015), mammals, reptiles and amphibians (IUCN, 2016) with an equal-area grid (approximately 1-degree or 110 x 110 km at the equator). Global-scale biodiversity data based on extent of occurrence should not be downscaled to less than 1 degree as finer resolutions lead to an over-estimation of species occurrences (Hurlbert & Jetz, 2007). Therefore, while our land system maps allow to assess relative percent change

at a 1 km<sup>2</sup> resolution, when estimating the loss in terms of actual species numbers, we use a 110 km grid as it is the finest resolution that is currently acceptable.

#### **2.4 Estimating the impact of agricultural development pathways on biodiversity**

We assessed species responses to various forms of land use and land-use intensity change. This data originates from the PREDICTS project, an initiative that collates local-scale studies from around the globe with the goal of quantifying species- and community-level responses to a range of human activities including: agriculture, hunting, deforestation, introduction of invasive species and human population expansion (Hudson *et al.*, 2014). Using 320,924 records of species richness and 1,130,251 records of abundance at 11,525 sites, estimates of species richness, rarefied species richness, and abundance percent change for various land-use categories (from a natural baseline) were calculated by Newbold *et al.* (2015).

To investigate the spatial patterns of biodiversity loss for each agricultural development pathway, we first matched our land systems classes to levels of high, medium, and low intensity for each major land use type (for detailed conversion table see Newbold *et al.*, 2015). This allowed us to calculate average biodiversity loss per land system (from an unimpacted baseline) by taking the mean model estimates of biodiversity loss per land-use intensity class from Newbold *et al.* (2015). The result gives average relative biodiversity gain or loss per land system (Table SI IV-3). We then calculated the biodiversity percent change per land system *conversion* in each of our three pathways described above (Table SI IV-4). We estimated biodiversity percent net change by taking the difference between land systems, divided by the original land system, this gave the relative biodiversity change on a 1-km grid as a result of shifting from one land system to another.

To calculate biodiversity loss in terms of the potential number of species lost per 110 km grid cell, we first calculated the area-weighted mean value of biodiversity percent change across all converted land systems per 110 km grid cell. We then multiplied this by the number of species present in each grid cell as derived from the extent of occurrence maps. Spatially explicit biodiversity data on abundance is not available on a global scale, so these values were not converted from relative (% per land system) to absolute values (number of individuals or biomass lost). We also calculated the top 5% and 10% of the distribution of species richness loss in order to highlight the highest risk regions for each pathway. Rarefied species richness allows for the comparison of areas in which densities differ, and was estimated by relative, percent change per land system. Results for rarefied species richness

showed weaker but mostly similar patterns as species richness and we therefore only show these results in the supplementary material (Table SI IV-4).

## **2.5 Analysing spatial patterns of biodiversity loss due to agricultural land-use change**

We spatially compared the overlap between our biodiversity loss estimates, in terms of top 5% and 10% of the distribution of species richness loss per pathway, with IUCN category protected areas (UNEP-WCMC, 2016) and three global conservation priority schemes: (1) the Conservation International (CI) biodiversity hotspots, as a reactive approach that targets areas which have already lost 70% of native habitat (Mittermeier *et al.*, 2004), (2) the global 200 ecoregions, as a mixture of both proactive and reactive approaches that identifies ecoregions of exceptional biodiversity in terms of irreplaceability and distinctiveness (Olson & Dinerstein, 2002), and (3) the last of the wild, a reactive approach which shows the ten largest contiguous wilderness areas by terrestrial biome and realm (Sanderson *et al.*, 2002). Together, this allowed us to ascertain whether our high-risk areas are recognised under global proactive and reactive conservation priority schemes or, in the case of protected areas, secure against potentially rising land-use pressure.

Finally, we summarized our results at the national level, since most conservation funding originates from domestic spending (\$14.5bn out of \$16bn), with approximately \$1bn from international NGOs (Waldron *et al.*, 2013). Thus, conveying results in relation to national contexts allows us to better understand policy relevant conservation opportunities. We calculated the average species richness lost per 110 km grid cell on each agricultural development pathway per country. In order to emphasize countries that are at higher risk, not only to potential species loss, but also in terms of national support for conservation and agricultural trends, we compared our results against (1) conservation spending, averaged per km<sup>2</sup> and corrected by the each countries' proportional dollar costs of a fixed basket of goods and services (from Waldron *et al.*, 2013), and (2) the average percent agricultural economic growth from 2009 to 2013 (World Bank Group, 2013). The latter gives an indication of countries with high agricultural growth rates, where conservation planning may therefore be more urgent. To objectively evaluate the ranking of countries in relation to species loss, conservation spending, and agricultural growth trends, we calculated z-scores of each variable, re-scaled them to be between 0 and 1 and then summed them. The use of z-scores is an established method for producing composite measures (Andersen *et al.*, 2006).

### **3 Results**

In general, the tropics, particularly the Amazon basin and Sub-Saharan Africa, had the highest risk of biodiversity loss, were only partially covered by protected areas and conservation prioritisation schemes, and were characterised by relatively low conservation funding and high agricultural growth.

#### **3.1 Expansion effects on biodiversity**

For pathways of expansion, mosaic grasslands and dense forests exhibited the highest overall relative biodiversity losses (up to 25% loss of species richness, Figure IV-1, Table SI IV-4). Areas of highest potential species richness loss due to expansion, in terms of the top 5% of species lost, resulting in between 167 - 264 species lost per 110 km grid cell, were overwhelmingly found in the Amazon Basin and the North-eastern Congolian forests and savannas (Figure IV-2). In terms of abundance loss, many regions in the tropics and the boreal forests were found to be at particularly high risk (21% loss of abundance in terms of the maximum percent loss per land system conversion)

#### **3.2 Intensification effects on biodiversity**

Overall, intensification effects on biodiversity were less than the effects of expansion. In terms of relative percent loss per land system conversion, land-use intensification resulted in up to 7% loss in species richness, spanning across much of Eastern Europe, India, Nepal and Sub-Saharan Africa (Figure IV-1, Table SI IV-4). In terms of the maximum number of species lost per 110 km grid cell, up to 19 species would be lost due to intensification across a large region of Eastern Europe and up to 34 species in India and Nepal. More concentrated regions of species richness loss were found in Mesoamerica, the Gran Chaco, and the Chiquitano dry forests of Bolivia, where 39 species would be lost. The top 5% of potential losses in species richness due to intensification would see between 33 and 60 species lost per grid cell in many regions of Sub-Saharan Africa, including the Eastern Guinean Forest-Savanna Mosaic and West Sudanian Savannah (42 species) and the Afromontane and the African Great Lakes Region (60 species; Figure IV-2). In terms of abundance losses, we found large areas spanning many parts of Eastern Europe, Russia, India and Sub-Saharan Africa that could lose up to 13% abundance under the intensification pathway (Figure IV-1).

#### **3.3 Combined effects of intensification and expansion on biodiversity**

As can be expected, the effect of the combination of expansion and intensification had the greatest negative effect on biodiversity (Figure IV-1). For most of the globe, since the risk

of biodiversity loss due to intensification is much less than the risk due to expansion (Figure IV-1), our combined pathway highlights many of the same areas as our pathway of expansion, especially when looking at the top 5 and 10% of the distribution of species loss. In terms of the top 5% of species lost, 184 - 317 species were found to be lost per 110 km grid cell (a loss of up to 30% of relative species richness), and include the majority of the Amazon Basin, a large area in the north east of the Democratic Republic of the Congo (DRC), smaller areas in Zambia and southern Tanzania, along with border regions of the Central African Republic, the Republic of the Congo, Cameroon and Gabon (Figure IV-2). Many parts of these areas also would withstand relative abundance losses of 31% under this pathway (Figure IV-1). Our 110 km grid cell under most risk globally was found in the Southwest Amazon moist forests in Peru, where a combination of expansion and intensification would result in the loss of 317 species of terrestrial vertebrates (Figure IV-2b).

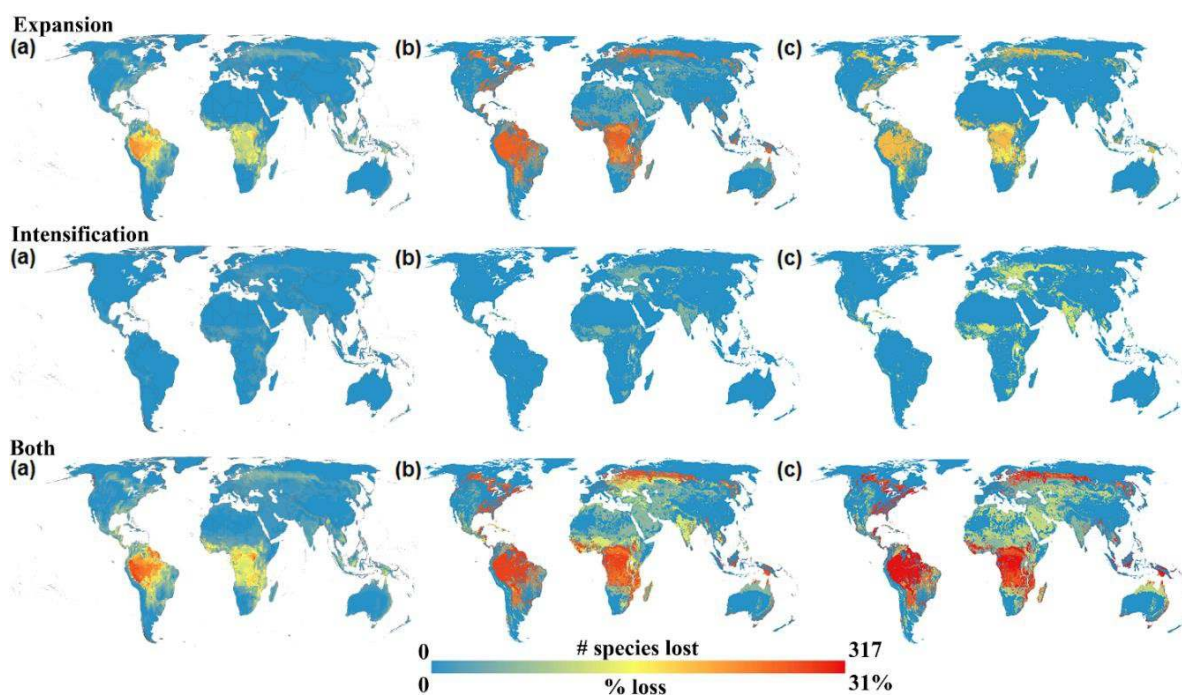


Figure IV-1: Biodiversity loss due to three agricultural development pathways in terms of: (a) the number of terrestrial vertebrate species (mammals, birds, amphibians and reptiles) lost per 110 km grid cell, (b) relative percent of species richness lost, (c) relative percent of abundance lost.

### 3.4 Comparison to protected areas and conservation priorities

Many regions of potentially high biodiversity risk due to our pathways of intensification and expansion are currently outside the protected area network (Figure IV-2a). In terms of expansion, we found the northeast of the DRC particularly at risk with over 200 estimated species lost per grid cell and up to a 31% loss of biodiversity abundance. Very few protected areas exist in this region, and of that, even fewer have a strict designation according to the



IUCN categorization (Figure IV-2a). The Amazon has an extensive network of protected areas, but is by no means fully protected. Our 110 km grid cell of highest risk for species loss occurred in the Southwest Amazon moist forests in Peru (317 species potentially lost), is partially but not entirely covered by the IUCN category II Bahuaja-Sonene and category VI Tambopata National Parks (Figure IV-2b). In sum, many of the areas we identify here were not fully protected, including our most at risk regions.

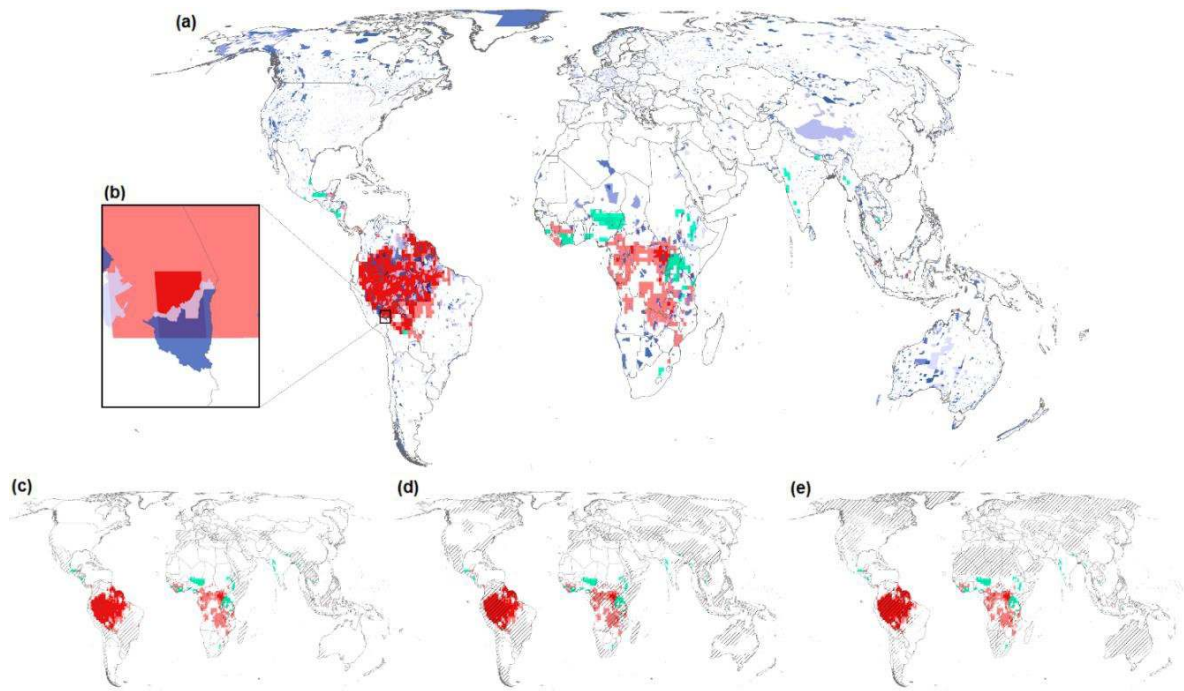


Figure IV-2: High-risk regions of species loss in terms of pathways of expansion (dark red = top 5%, light red = top 10%) and intensification (dark turquoise = top 5%, light turquoise = top 10%) overlaid with: (a) protected areas (IUCN category I to IV, darker blue denotes higher protection), (b) the 110 km grid cell most at risk of species richness loss found in the moist forests of Peru and partially covered by the IUCN category II Bahuaja-Sonene and cat VI Tambopata National Reserve. Bottom Panel: conservation priority schemes (dashed lines), (c) Conservation International hotspots (Mittermeier *et al.*, 2004), (d) Global 200 Ecoregions (Olson & Dinerstein, 2002) and, (e) Last of the Wild (Sanderson *et al.*, 2002).

In terms of conservation prioritization schemes and their overlap with our high risk regions (top 10% of species richness loss per pathway), we found that, on average, less than half of our high risk regions were included under some form of conservation prioritization. Pathways of (1) expansion and (2) combined intensification and expansion, highlighted very similar top 10% at risk regions and are thus referred to as ‘high-risk regions of expansion’. Conservation International (CI) hotspots overlapped with 36% of our high-risk regions of intensification, mostly in pockets of South East Asia and Mesoamerica, and with less than

7% of high-risk regions of expansion (Figure IV-2c). The Global 200 ecoregions coincided with many of our regions of high-risk regions of intensification (35%) and most notably across most of our high-risk regions of expansion (75%, Figure IV-2d). Finally, the Last of the Wild coincided with less than 1% of our high-risk regions of intensification and 60% of our high-risk regions of expansion, this overlap was found in many parts of Latin America but to a lesser degree in Sub-Saharan Africa (Figure IV-2e).

### 3.5 National level summaries

Sub-Saharan African and Latin American countries dominated the top ten ranks in terms of average species and abundance loss. Suriname had the overall highest potential species richness loss (average 212 to 219 species lost per 110 km grid cell under the expansion and combined pathway respectively, Table IV-2). Rwanda was worst affected by our intensification pathway with an average of 51 species lost per 110 km grid cell. The Republic of the Congo and the DRC ranked highly across pathways of expansion. Outside of the tropics, the only countries to reach the top ten were in Eastern Europe, where Moldova and the Ukraine were found to lose an average of 10% in abundance of species under the intensification pathway (Table IV-2).

Table IV-2: Top ten at risk countries in terms of highest average biodiversity loss (SR – species richness, Abundance - % abundance change relative to baseline) for our three main pathways (both – combination of expansion and intensification).

Top Ten	Intensification		Expansion		Both	
	SR	Abundance	SR	Abundance	SR	Abundance
1	Rwanda	Mayotte	Suriname	Rep. of Congo	Suriname	Rep. of Congo
2	Burundi	Haiti	Fr. Guiana	DRC	Fr. Guiana	DRC
3	Uganda	Rwanda	Guyana	Suriname	Guyana	Suriname
4	El Salvador	Moldova	R. Congo	Bahamas	R. Congo	Liberia
5	Togo	Ukraine	DRC	Gabon	DRC	C. African Rep.
6	Nigeria	Burundi	Liberia	Liberia	Liberia	Bahamas
7	Sierra Leone	El Salvador	Gabon	Fr. Guiana	Gabon	Gabon
8	Ivory Coast	St. Lucia	Zambia	C. African Rep.	Zambia	Fr. Guiana
9	Malawi	Barbados	Cameroon	Guyana	Cameroon	Zambia
10	Nicaragua	Uganda	Belize	Eq. Guinea	Belize	Guyana

Countries that spend most on conservation per km<sup>2</sup>, like the Netherlands, Switzerland and Belgium had a comparatively low risk of species loss due to future agricultural land-use change for all of our three agricultural pathways. This is likely because most suitable agricultural land is already utilised and such countries have low species richness in comparison to the tropics. The highest risk for species loss due to agricultural land-use change occurred in less economically developed and highly biodiverse countries which also have much lower conservation investment. Among countries with low spending but high potential species loss due to intensification, Togo, Sierra Leone, Coted'Ivoire and Moldova stood out (Figure IV-3b).

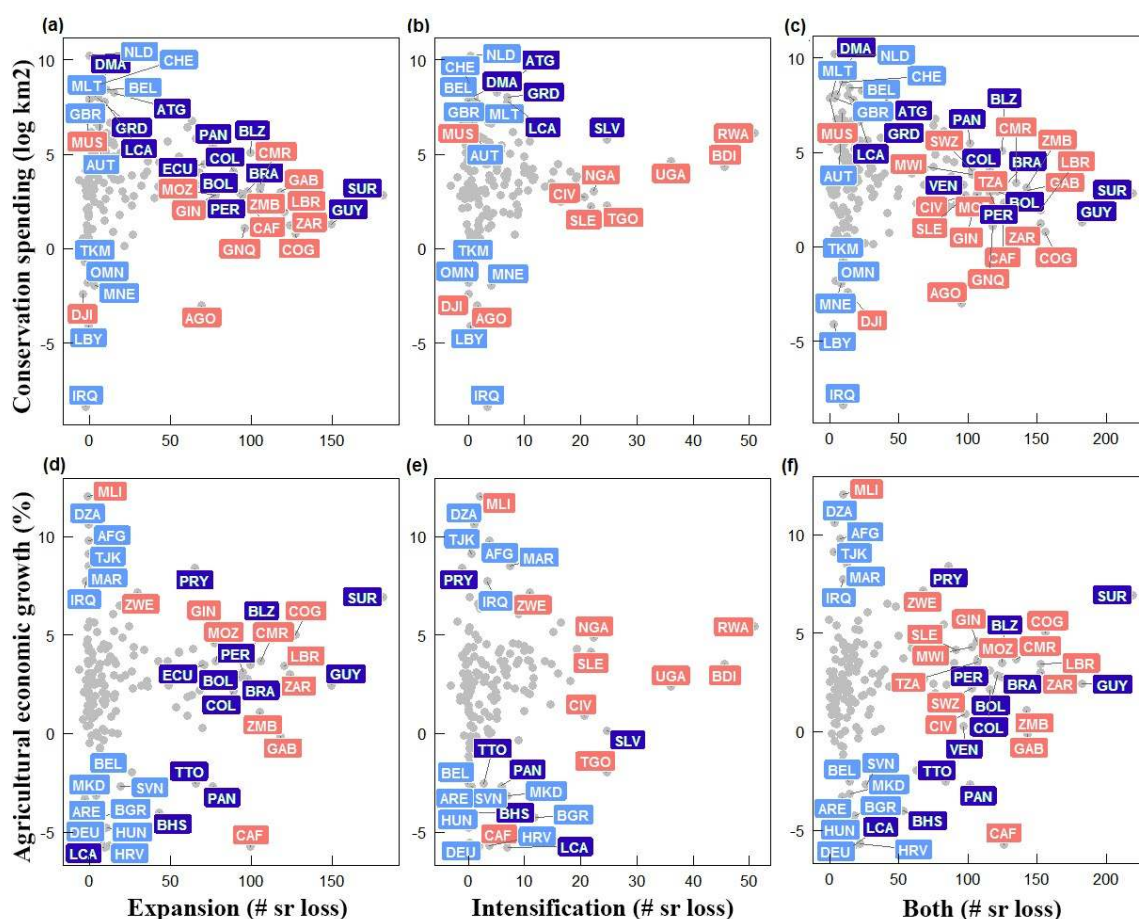


Figure IV-3: Average national level species richness lost per 110 km grid cell (# sr loss) on each pathway (expansion, intensification, and both expansion and intensification) compared with the natural log of conservation spending per km<sup>2</sup> at the national level – log spending (Waldron *et al.*, 2013), and the average % economic growth of the agricultural sector of 2009-2013 – agricultural growth (World Bank Group, 2013). Colour code according to each country's realm (Afrotropical = Red, Neotropical = Navy, Palearctic = Blue). Country codes for countries referred to in the text: Angola = AGO, Belgium = BEL, Congo, Dem. Rep. = ZAR, Congo, Rep. = COG, Cote d'Ivoire = CIV, Equatorial Guinea = GNQ, Guinea, Rep. of = GIN, Guyana = GUY, Liberia = LBR, Moldova = MDA, Netherlands = NLD, Nigeria = NGA, Paraguay = PRY, Rwanda = RWA, Sierra Leone = SLE, Switzerland = CHE, Togo = TGO, Ukraine = UKR. All others in Table SI IV-5.

Whereas, Angola, Rep. of Congo, DRC and Guyana were among those with low spending and high species loss related to pathways of expansion (Figure IV-3a-c). The majority of countries that we found to be at-risk of high biodiversity loss along with below-average conservation funding per km<sup>2</sup> were not represented on Waldron et al's (2013) top 40 severely underfunded countries, particularly the DRC, Equatorial Guinea, Liberia and Suriname (see Table SI IV-5 & Table SI IV-6 for full list).

Among countries where agricultural growth was high in 2009-2013, meaning that future agricultural development is likely, and which also would lose high levels of species due to intensification, Rwanda, Moldova, Nigeria stood out. Countries with high species loss due to pathways of expansion and high agricultural growth included: Suriname, Paraguay, Rep. of Congo and Rep. of Guinea (Figure IV-3d-f).

#### **4 Discussion**

With a growing consensus that both expansion and intensification are likely to continue in the future, and that these changes will be a key driver of biodiversity loss throughout the 21<sup>st</sup> century, investigating which areas are most at risk has become central to conservation research (Green *et al.*, 2005; Phalan *et al.*, 2014). We provide a robust and transparent mechanism for estimating biodiversity loss under possible pathways of future agricultural land-use change in order to show which areas are susceptible to what forms of potential land-use change. A major gap in sustainability research lies in linking the local scale effects of land use on biodiversity to the impact of broader scale pathways of potential future land-use change. We bridge this gap by estimating both fine-scale, percentage-based biodiversity loss, and then aggregating and translating these losses to the potential number of species lost on a 110 km grid to a national level. By using absolute values, we can estimate local, 110 km grid-scale extinction, for many small-ranged threatened species global extinctions are also likely – depending on the spatial extent of land-use change.

While using absolute values has the advantage of highlighting particularly biodiverse regions at risk, relative values can work on a finer-scale 1km grid and highlight areas with considerable implications. For example, when comparing our relative loss results from a natural baseline, both pathways of intensification and expansion result in over 20% loss of species richness (Table SI IV-3 and Table SI IV-4), this likely passes the safe limits of planetary boundaries and considerably impairs the ability of biodiversity to contribute towards ecosystem function and services, and thus to human well-being (Hooper *et al.*, 2012;

Newbold *et al.*, 2016). Furthermore, relative values don't overlook the importance of cultural landscapes – such areas include those that are not found to be hugely relevant on global scale, however, this does not imply that high percentage loss is not worth intervention. For example, many low-intensity culturally significant landscapes in Eastern Europe are high in agricultural biodiversity that would be lost if industrialised intensification were to occur (Donald *et al.*, 2002; Hartel *et al.*, 2010).

The global protected area network is designed to achieve the long term conservation of nature with associated ecosystem services and cultural values (IUCN, 2008). Comparing our top 5 and 10% at risk areas to this network showed some overlap, yet none of our high-risk areas were fully protected. Our results are especially useful in highlighting areas where we find a fragmented arrangement of mostly unconnected protected areas alongside our high-risk areas (Figure IV-2). For instance, in the moist forests of Peru, where protected areas and buffer zones only cover half of the most-threatened 110 km grid cell (Figure IV-2b).

Our areas at risk had little overlap with many conservation priority schemes, particularly the more reactive approaches, such as CI Hotspots (Mittermeier *et al.*, 2004). CI Hotspots were defined based on a single taxonomic group (i.e., plants) and the amount of remaining habitat, but do not factor in potential future loss. A substantial proportion of conservation funding is directed towards CI hotspots (Brooks *et al.*, 2006), but our results suggest that they may not be particularly effective in protecting vertebrates from agricultural land-use change. Many at risk areas were also not covered by the more proactive conservation prioritization schemes, such as the Last of the Wild, which showed little overlap with our high-risk areas in Sub-Saharan Africa (Figure IV-2e). This is understandable for areas that are threatened by agricultural intensification, since these areas would not be classified as 'wild', but a number of currently intact habitats such as Congolian forests and savannas, that we found to be highly susceptible to expansion impacts were also not covered under this scheme. Specific conservation prioritization is needed in terms of potential future land-use pressures in order to avoid overlooking such highly biodiverse at risk areas.

Considering the significant proportion of conservation funding spent at national scale (Waldron *et al.*, 2013), investigating which countries are most at risk in terms of both relative conservation funding and potential biodiversity loss is a worthwhile pursuit. Our results identify investment opportunities to avoid potentially high biodiversity loss that may be particularly urgent due to underfunding and high agricultural growth rates. In general, across all scales our forward looking approach is particularly relevant with regard to conservation

planning, where delayed mitigation efforts are likely to have a lower rate of success, take longer to implement, and cost more than prompt action (Cook *et al.*, 2014; Oliver & Roy, 2015).

Our results are in line with other broad-scale studies that assess potential conservation conflict due to future agricultural land-use change. We found many regions of India and the African Great Lakes to be areas of high potential conservation conflict, similar to the work of others that highlighted these regions based on high levels of human appropriation of net primary productivity and cropland extent alongside high levels of vertebrate endemism richness (Kehoe *et al.*, 2015), high numbers of threatened vertebrates and the proportion of non-cropland that could be degraded (Shackelford *et al.*, 2015), and one of the highest priorities for both intensification and bird conservation – particularly for the African Great Lakes region (Phalan *et al.*, 2014). This emphasizes the importance of ramping up conservation efforts in these regions to curb possible future biodiversity loss. Latin America and Sub-Saharan Africa contains relatively intact and highly diverse natural areas that are suitable for cropland. Thus, the potential for agricultural activity and subsequent biodiversity loss is high. These areas, particularly Sub-Saharan Africa, are in the cross hairs of economic, demographic and agricultural growth, making the minimization of the potential impacts of agricultural change an urgent task (Searchinger *et al.*, 2015; Estes *et al.*, 2016). Finally, our results also show that compared to other studies (Shackelford *et al.*, 2015), South-East Asia has relatively low estimated biodiversity loss. This may be because this region is more heavily comprised of mosaic cropland, with the remaining natural areas either relatively small or unsuitable for cropland (Figure SI IV-1). This may also explain the discrepancy between our results and Shackelford *et al.* (2015), where areas that are not suitable for cropland were not excluded from the analysis.

A few sources of uncertainty need mentioning. First, our analyses ignores lagged responses and thus possible extinction debt as historical data are rare (Newbold *et al.*, 2015), and are therefore a conservative estimate of biodiversity loss (Kuussaari *et al.*, 2009). Second, although our method for estimating biodiversity impacts is based on the largest dataset of land use related biodiversity change, a number of countries and ecosystems were under-represented (Hudson *et al.*, 2014). Third, our intensification pathways may overestimate biodiversity loss, because they assume that conventional intensification will take place. Intensification is complex and multi-dimensional (Kuemmerle *et al.*, 2013; Kehoe *et al.*, 2015), and there is a number of ways in which yield increases can occur with lower or no net loss of species richness and abundance (Clough *et al.*, 2011; Tschardtke *et al.*, 2012). In

order to estimate biodiversity change associated with ‘sustainable’ intensification, it is necessary to both develop a better definition of this concept along with more empirical data, particularly when considering fragile ecosystems (Loos *et al.*, 2014). Fourth, the underlying land systems map is built on land cover maps that can have significantly different spatial extents, and some lack formal validation (Fritz *et al.*, 2011; Verburg *et al.*, 2011), which can translate into errors in the assessment of potential biodiversity impacts. No global datasets are currently available indicating areas suitable for livestock; therefore, livestock expansion was not explicitly included in the analysis. Moreover, data protection and confidentiality legislation make it difficult to map industrialised livestock units (Wint & Robinson, 2007) and assess their impact on biodiversity. Fifth and finally, our prioritisation is based on maximising for species richness and abundance, this cannot and should not be the only way to prioritise for nature conservation, especially when considering the importance of intrinsic and cultural values along with ecosystem resilience and human well-being (Fischer *et al.*, 2014). Species richness is particularly problematic as it can be over-representative of common, widespread species and can overshadow rare or small-ranged species, which are often most in need of conservation (Grenyer *et al.*, 2006). With better data, for example, on the effect of land-use change on threatened species, we could highlight areas that are particularly sensitive to change.

In sum, our results can inform policy and future analysis by highlighting the most at risk areas from 1km<sup>2</sup> to the national level where the threat to species richness and abundance related to potential future land-use change was previously unknown. This methodology compliments scenario-based methods by providing an overview of areas most at risk under the main modes of agricultural change. In a world of rapidly increasing demand on natural resources, our proactive approach serves to indicate where timely conservation action could avert future biodiversity loss. Although our results should not be directly used to guide conservation action, they support previous calls that potential future threats due to land-use change should be incorporated in conservation prioritization schemes (Lee & Jetz, 2008; Visconti *et al.*, 2011; Tingley *et al.*, 2013).

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Our updated global land systems map and all percentage-based results are open access and available from HU datahub. This research contributes to the Global Land Project ([www.globallandproject.org](http://www.globallandproject.org)).



### Supplementary Information

Figure SI IV-1: Global Land System classification used in this analyses (~1km resolution). Darker green areas indicate predominantly natural regions of forest and grassland that are not suitable for cropland. Lighter green systems annotated with (CS) indicate areas where cropland is suitable – but not currently present. Full dataset available for download from HU datahub.

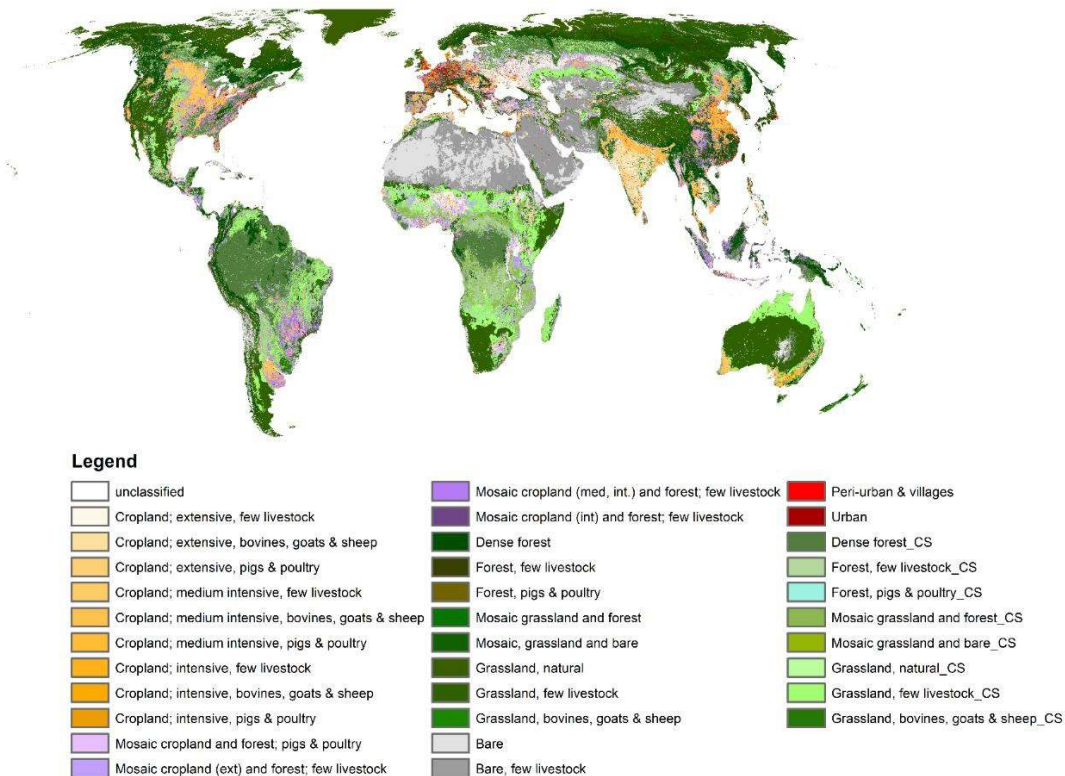


Figure SI IV-2: Hierarchical classification procedure to delineate Land Systems. Classification thresholds are given in the rectangles, pp = pigs & poultry (nr/km<sup>2</sup>), bgs = bovines, goats & sheep (nr/km<sup>2</sup>), eff = efficiency of agricultural production (int1 = extensive system, int2 = medium intensive system, int3 = intensive system), built-up, bare, crop and tree cover in percentages.

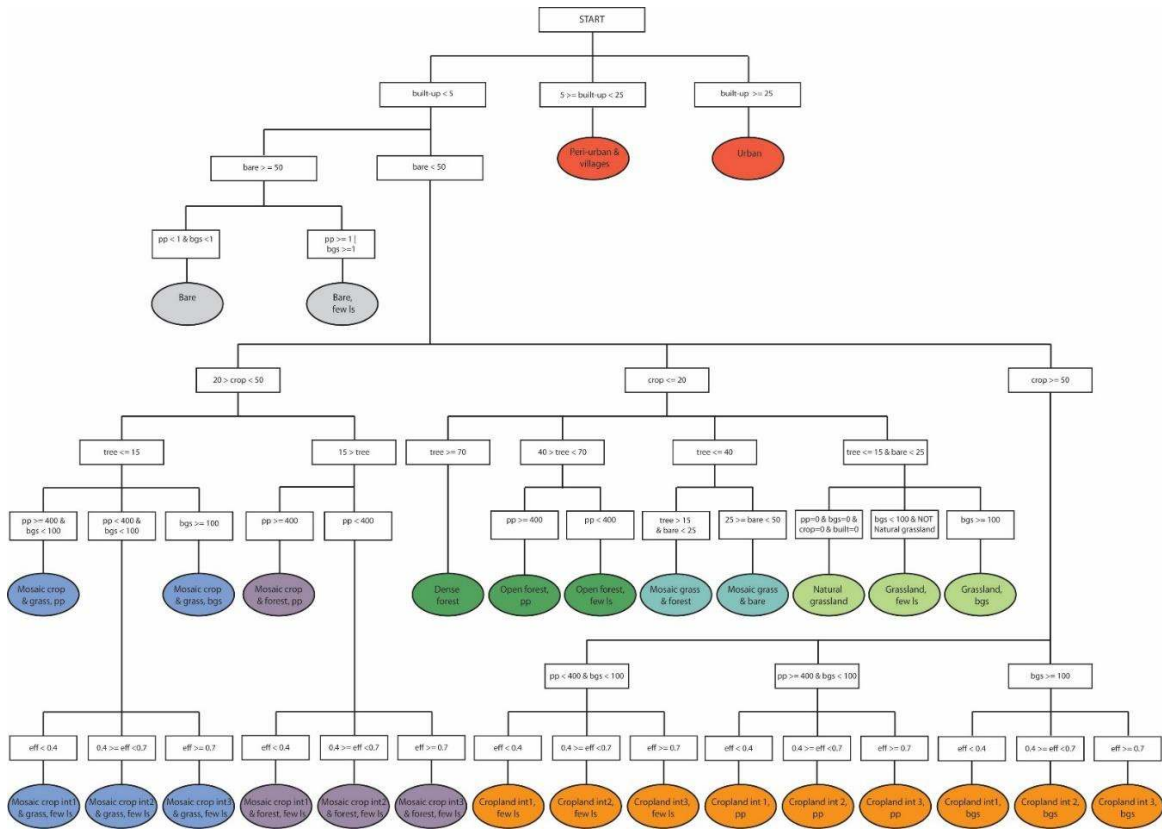


Table SI IV-1: Details on datasets for the Global Land System map V2

	<i>Dataset</i> <i>(citation, original scale)</i>	<i>Description</i> <i>(data value, reference year)</i>	<i>Data Source</i>
INPUT METRICS	<b>Cropland</b> - (Fritz et al., 2015, 1km)	(% per grid cell, 2005)	IIASA-IFPRI Cropland Map see publication: <a href="http://onlinelibrary.wiley.com/doi/10.1111/gcb.12838/abstract">http://onlinelibrary.wiley.com/doi/10.1111/gcb.12838/abstract</a>
	<b>Tree Cover</b> (Hansen et al. 2013, 1 arc-second per pixel, or ~ 30 meters per pixel at the equator)	(% per grid cell, ~2000)	Time-series analysis of Landsat images <a href="http://earthenginepartners.appspot.com/science-2013-global-forest">http://earthenginepartners.appspot.com/science-2013-global-forest</a>
	<b>Urban and Bare Areas</b> (Land Cover CCI, 2016, 300m)	(% per grid cell, 2008-2012).	CCI-LC project ESA
	<b>Livestock densities*</b> - Gridded livestock of the world (Wint & Robinson, 2007, 0.05°)	Livestock heads accounting for amount of land suitable for livestock production (livestock heads per km <sup>2</sup> , ~2000)	FAO and spatially predicted on suitable land
SYSTEM METRICS	<b>Crop Suitability</b> - (Fischer et al. 2012 - 2012, 5 arc min)	Crop suitability index (class) for high input level rain-fed cereals (1961-1990)	FAO/IIASA, 2011-2012. Global Agro-ecological Zones (GAEZ v3.0)
	<b>Yield Gaps</b> - (FAO/IIASA, 2011-2012, 5 arc min)	Ratio of actual and potential yield for high input level main crops (2000)	FAO/IIASA, 2011-2012. Global Agro-ecological Zones (GAEZ v3.0)

\* An updated recent publication for livestock densities is now available from Robinson *et al.* (2014) was not utilized due to what appeared to be a lower spatial resolution in many regions, especially in Sub-Saharan Africa.

Table SI IV-2: Land system conversions for each pathway \*Classes 9 –13 (Mosaic cropland and grassland classes) no longer occur in our updated land systems classifications as we use the same decision tree from Van Assellen but with new datasets comprising of different, often higher, values.)

<b>Land Systems Name Key</b>	<b>Original</b>			<b>Expansion &amp;</b>
	<b>Land System</b>	<b>Intensification Land System</b>	<b>Expansion Land System</b>	<b>Intensification Land System</b>
0. Cropland ext, few ls	VALUE 0	VALUE 6	-	VALUE 6
1. Cropland ext, bgs	VALUE 1	VALUE 7	-	VALUE 7
2. Cropland ext, pp	VALUE 2	VALUE 8	-	VALUE 8
3. Cropland m. int, few ls	VALUE 3	VALUE 6	-	VALUE 6
4. Cropland m. int, bgs	VALUE 4	VALUE 7	-	VALUE 7
5. Cropland m. int, pp	VALUE 5	VALUE 8	-	VALUE 8
6. Cropland int, few ls	VALUE 6	-	-	-
7. Cropland int, bgs	VALUE 7	-	-	-
8. Cropland int, pp	VALUE 8	-	-	-
9. Mosaic cropland and grassland, bgs	VALUE 9	VALUE 7	-	VALUE 7
10. Mosaic cropland and grassland, pp	VALUE 10	VALUE 8	-	VALUE 8
11. Mosaic cropland ext and grassland, few ls	VALUE 11	VALUE 6	-	VALUE 6
12. Mosaic cropland m. int and grassland, few ls	VALUE 12	VALUE 6	-	VALUE 6
13. Mosaic cropland int and grassland, few ls	VALUE 13	VALUE 6	-	VALUE 6
14. Mosaic cropland and forest, pp	VALUE 14	VALUE 8	-	VALUE 8
15. Mosaic cropland ext and open forest, few ls	VALUE 15	VALUE 6	-	VALUE 6
16. Mosaic cropland m. int and open forest, few ls	VALUE 16	VALUE 6	-	VALUE 6
17. Mosaic cropland int and open forest, few ls	VALUE 17	VALUE 6	-	VALUE 6
18. Dense forest	VALUE 18	-	VALUE 0	VALUE 6
19. Open forest, few ls	VALUE 19	-	VALUE 0	VALUE 6
20. Open forest, pp	VALUE 20	-	VALUE 1	VALUE 8
21. Mosaic grassland and open forest	VALUE 21	-	VALUE 0	VALUE 6
22. Mosaic grassland and bare	VALUE 22	-	VALUE 0	VALUE 6
23. Natural grassland	VALUE 23	-	VALUE 0	VALUE 6
24. Grassland, few ls	VALUE 24	-	VALUE 0	VALUE 6
25. Grassland, bgs	VALUE 25	-	VALUE 1	VALUE 7

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26. Bare	VALUE 26 -	-	-
27. Bare,few ls	VALUE 27 -	VALUE 0	VALUE 6
28. Peri-urban & villages	VALUE 28 -	-	-
29. Urban	VALUE 29 -	-	-

Table SI IV-3: Modelled mean estimates (following Newbold et al. 2015) of relative percent biodiversity change for each Land System. Values represent the percentage of remaining biodiversity, expressed in terms of total species richness (SR) and rarefied species richness (Rarefied SR) and abundance. All values are relative to an un-impacted baseline (primary vegetation, minimal intensity of use, zero human population density, and maximum observed distance to roads and travel time to major city). First numbers give modelled mean estimates and numbers in brackets the 95% confidence limits (under tenfold cross-validation, excluding data from approximately 10% of studies at a time.)

<b>Land System</b>	<b>SR (CI)</b>	<b>Rarefied SR (CI)</b>	<b>Abundance (CI)</b>
0. Cropland ext, few ls	71.85 (62.65 – 82.35)	79.85 (69.7 – 91.45)	80.80 (62.60 - 104.20)
1. Cropland ext, bgs	68 (57.4 – 80.7)	76.75 (65.95 – 89.25)	77.25 (56.65 - 105.70)
2. Cropland ext, pp	68 (57.4 – 80.7)	76.75 (65.95 – 89.25)	77.25 (56.65 - 105.70)
3. Cropland med. Int, few ls	66.25 (56.85 - 77.2)	80.65 (70.75 - 91.85)	63.55 (48.05 - 84.05)
4. Cropland med. int, bgs	62.4 (51.6 - 75.55)	77.55 (67 - 89.65)	60.00 (42.10 - 85.55)
5. Cropland med. int, pp	62.4 (51.6 - 75.55)	77.55 (67 - 89.65)	60.00 (42.10 - 85.55)
6. Cropland int, few ls	67.15 (56.95 - 79.25)	76.85 (67.35 - 87.75)	70.45 (51.55 - 96.60)
7. Cropland int, bgs	63.3 (51.7 - 77.6)	73.75 (63.6 - 85.55)	66.90 (45.60 - 98.10)
8. Cropland int, pp	63.3 (51.7 - 77.6)	73.75 (63.6 - 85.55)	66.90 (45.60 - 98.10)
15. Mosaic cropland and forest, pp	63.3 (51.7 - 77.6)	73.75 (63.6 - 85.55)	66.90 (45.60 - 98.10)
16. Mosaic cropland ext and open forest, few ls	71.85 (62.65 - 82.35)	79.85 (69.7 - 91.45)	80.80 (62.60 - 104.20)
17. Mosaic cropland m. int and open forest, few ls	66.25 (56.85 - 77.2)	80.65 (70.75 - 91.85)	63.55 (48.05 - 84.05)
18. Mosaic cropland int and open forest, few ls	67.15 (56.95 - 79.25)	76.85 (67.35 - 87.75)	70.45 (51.55 - 96.60)
19. Dense forest	96.13 (90.54 - 100.39)	97 (92.59 - 99.09)	98.03 (88.28 - 108.28)
20. Open forest, few ls	89.23 (79.54 - 100.19)	92.71 (82.64 - 99.47)	90.96 (71.44 - 104.63)
21. Open forest, pp	88 (75.34 - 102.92)	89.41 (77.54 - 98.57)	97.56 (70.81 - 122.80)
22. Mosaic grassland and open forest	96.13	97	98.03

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	(90.54 - 100.39)	(92.59 - 99.09)	(88.28 - 108.28)
23. Mosaic grassland and bare	96.13	97	98.03
	(90.54 - 100.39)	(92.59 - 99.09)	(88.28 - 108.28)
24. Natural grassland	96.13	97	98.03
	(90.54 - 100.39)	(92.59 - 99.09)	(88.28 - 108.28)
25. Grassland, few ls	70.6	82.2	72.20
	(61.3 - 81.2)	(73.3 - 92.1)	(56.00 - 93.00)
26. Grassland, bgs	62.9	76	65.10
	(50.8 - 77.9)	(65.8 - 87.7)	(44.10 - 96.00)
27. Bare, few ls	70.6	82.2	72.20
	(61.3 - 81.2)	(73.3 - 92.1)	(56.00 - 93.00)
28. Peri-urban & villages	96	109.7	81.80
	(79.4 - 116)	(84.9 - 141.8)	(51.60 - 129.70)
29. Urban	49.8	71.1	37.60
	(37.5 - 66)	(54.9 - 92.1)	(21.10 - 67.20)

Table SI IV-4: Modelled mean estimates of relative percent biodiversity loss (SR – species richness, Ab. – abundance) according to agricultural development pathways (Both - intensification and expansion). Note: Minus numbers signify a gain in species richness and abundance, however, these land systems are generally located in areas that are of relatively low species richness and abundance.

Land System	Expansion			Intensification			Both		
	SR	Abundance	Rarefied SR	SR	Abundance	Rarefied SR	SR	Abundance	Rarefied SR
0. Cropland ext, few ls	-	-	-	6.54	12.81	3.76	6.54	12.81	3.76
1. Cropland ext, bgs	-	-	-	6.91	13.40	3.91	6.91	13.40	3.91
2. Cropland ext, pp	-	-	-	6.91	13.40	3.91	6.91	13.40	3.91
3. Cropland m. int, few ls	-	-	-	-1.36	-10.86	4.71	-1.36	-10.86	4.71
4. Cropland m. int, bgs	-	-	-	-1.44	-11.50	4.90	-1.44	-11.50	4.90
5. Cropland m. int, pp	-	-	-	-1.44	-11.50	4.90	-1.44	-11.50	4.90
6. Cropland int, few ls	-	-	-	-	-	-	-	-	-
7. Cropland int, bgs	-	-	-	-	-	-	-	-	-
8. Cropland int, pp	-	-	-	-	-	-	-	-	-
9. Mosaic cropland and grassland, bgs	-	-	-	-	-	-	-	-	-
10. Mosaic cropland and grassland, pp	-	-	-	-	-	-	-	-	-
11. Mosaic cropland ext and grassland, few ls	-	-	-	6.54	12.81	3.76	6.54	12.81	3.76
12. Mosaic cropland m. int and grassland, few ls	-	-	-	-1.36	-10.86	4.71	-1.36	-10.86	4.71
13. Mosaic cropland int and grassland, few ls	-	-	-	-	-	-	-	-	-
14. Mosaic cropland and forest, pp	-	-	-	-	-	-	-	-	-
15. Mosaic cropland ext and open forest, few ls	-	-	-	6.54	12.81	3.76	6.54	12.81	3.76



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16. Mosaic cropland m. int and open forest, few ls	-	-	-	-1.36	-10.86	4.71	-1.36	-10.86	4.71
17. Mosaic cropland int and open forest, few ls	-	-	-	-	-	-	-	-	-
18. Dense forest	25.26	17.58	17.68	-	-	-	30.15	28.14	20.77
19. Open forest, few ls	19.48	11.17	13.87	-	-	-	24.75	22.54	17.11
20. Open forest, pp	22.73	20.81	14.16	-	-	-	28.07	31.42	17.52
21. Mosaic grassland and open forest	25.26	17.58	17.68	-	-	-	30.15	28.14	20.77
22. Mosaic grassland and bare	25.26	17.58	17.68	-	-	-	30.15	28.14	20.77
23. Natural grassland	25.26	17.58	17.68	-	-	-	30.15	28.14	20.77
24. Grassland, few ls	-1.77	-11.91	2.86	-	-	-	4.89	2.42	6.51
25. Grassland, bgs	-8.11	-18.66	-0.99	-	-	-	-0.64	-2.76	2.96
26. Bare	-	-	-	-	-	-	-	-	-
27. Bare, few ls	-1.77	-11.91	2.86	-	-	-	4.89	2.42	6.51
28. Peri-urban & villages	-	-	-	-	-	-	-	-	-
29. Urban	-	-	-	-	-	-	-	-	-

Table SI IV-5: National level biodiversity loss in terms of average species richness (SR) and % abundance loss for each of the three agricultural pathways. Also shown are the average % average agricultural economic growth between 2009-2013 (World Bank Group, 2013), and conservation spending per km<sup>2</sup>, based on (Waldron *et al.*, 2013)

Country	Country Code	Intensification (SR)	Intensification (% Abundance)	Expansion (SR)	Expansion (% Abundance)	Both (SR)	Both (% Abundance)	Average % Agriculture growth 2009-2013	Spending / Km <sup>2</sup>	LN Spend / km <sup>2</sup>
Afghanistan	AFG	3.74	2.40	-0.81	-3.25	7.35	3.25	9.77	5.57	1.72
Albania	ALB	7.50	4.25	1.50	-0.25	11.00	4.75	4.08	153.51	5.03
Algeria	DZA	1.10	0.72		-3.82	3.29	1.52	10.60	1.82	0.60
Angola	AGO	1.59	0.48	69.28	5.98	95.13	16.86	0.00	0.05	-3.02
Antigua and Barbuda	ATG	5.00	6.00	15.00	6.00	23.00	16.00	1.83	3857.4	8.26
Argentina	ARG	-0.53	-2.00	9.67	-0.87	15.92	1.20	1.65	1	2.63
Armenia	ARM	10.00	5.00	-1.00	-2.00	14.50	6.00	4.22	13.91	4.39
Australia	AUS	-0.15	-0.74	6.79	-1.38	13.66	2.36	4.31	80.35	4.23
Austria	AUT	0.20	-0.60	6.40	0.80	9.00	2.00	-1.48	1244.7	7.13
Azerbaijan	AZE	8.54	4.93	6.00	-1.32	21.36	8.25	3.52	4	2.36
Bahamas, The	BHS	0.20	0.00	42.80	13.13	53.07	22.87	-3.99	10.63	4.58
Bangladesh	BGD	1.07	-4.29	12.43	1.14	18.00	-1.36	3.91	97.94	4.12
Barbados	BRB	8.00	9.00	1.00	0.00	10.00	9.00	0.00	61.33	6.18
Belgium	BEL	0.00	0.00	10.50	2.00	14.00	4.50	-2.53	484.44	8.45
Belize	BLZ	-0.50	-0.50	99.50	9.00	124.50	16.00	3.49	4671.0	5.08
Benin	BEN	18.18	6.18	35.09	2.09	68.09	14.09	2.67	3	4.11
Bhutan	BTN	4.88	0.47	7.94	0.53	14.35	1.76	2.12	160.83	4.61
Bolivia	BOL	3.07	0.74	92.73	6.44	121.05	14.86	2.88	61.09	2.95
Bosnia and Herzegovina	BIH	9.00	4.77	8.54	1.00	20.62	8.00	-0.32	19.18	3.48

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Botswana	BWA	0.24	0.07	1.59	-3.59	14.96	1.85	1.03	28.70	3.36
Brazil	BRA	-0.47	-1.26	97.46	6.81	124.38	13.91	2.78	21.35	3.06
Brunei	BRN	0.00	-1.00	63.00	6.00	76.00	9.00	1.96	897.91	6.80
Bulgaria	BGR	11.80	6.20	4.80	0.90	18.00	7.90	-4.26	44.66	3.80
Burkina Faso	BFA	10.59	4.18	-2.32	-7.05	29.41	6.73	2.07	21.99	3.09
Burma	MMR	3.29	-0.30	21.58	1.66	31.06	3.31	0.00	1.16	0.15
Burundi	BDI	45.67	10.00	16.33	1.00	66.67	12.33	3.54	78.23	4.36
Belarus	BLR	8.20	5.80	26.50	4.80	42.80	16.80	2.31	2.12	0.75
Cambodia	KHM	13.58	4.26	42.05	3.84	68.26	12.63	3.67	26.82	3.29
Cameroon	CMR	6.45	1.40	105.45	10.19	134.74	18.88	3.66	30.08	3.40
Canada	CAN	-0.17	-0.60	7.28	1.72	9.00	2.96	2.91	108.82	4.69
Central African Republic	CAF	1.82	0.65	99.55	12.08	125.80	23.18	-5.73	10.21	2.32
Chad, Claimed by Libya	TCD	1.90	0.81	1.45	-6.29	13.68	3.13	3.03	2.90	1.06
Chile	CHL	0.57	0.48	2.95	0.16	5.00	2.29	0.87	22.75	3.12
China	CHN	-0.51	-1.53	1.14	-0.86	2.42	-0.83	4.14	15.55	2.74
Colombia	COL	0.45	-0.36	88.70	5.78	115.60	12.89	2.13	59.87	4.09
Comoros	COM	4.50	8.00	0.50	0.00	5.00	8.50	1.69	28.49	3.35
Congo	COG	1.29	0.36	127.36	14.54	155.96	25.14	5.00	2.21	0.79
Congo Dem. Rep.	ZAR	1.81	0.42	123.92	14.32	152.53	24.98	3.00	3.43	1.23
Costa Rica	CRI	-1.38	-2.13	60.38	4.38	74.63	6.38	1.86	609.38	6.41
Croatia	HRV	3.67	1.83	12.00	0.83	21.67	6.83	-5.68	282.48	5.64
Cuba	CUB	11.54	7.38	19.27	3.92	36.12	14.92	2.81	39.89	3.69
Cyprus	CYP	-0.80	-2.20	-0.20	-0.40	0.00	-2.20	1.76	306.67	5.73
Czech Republic	CZE	-0.38	-3.38	8.13	1.50	10.00	0.13	1.67	245.71	5.50
Denmark	DNK	0.13	0.13	3.50	0.38	5.13	1.88	1.92	178.04	5.18
Djibouti	DJI	0.00	0.00	-4.33	-7.67	12.67	1.67	0.00	0.09	-2.37
									3196.0	
Dominica	DMA	1.00	1.00	3.00	1.00	5.00	3.00	2.63	5	8.07
Dominican Republic	DOM	8.88	5.75	14.25	3.25	27.25	12.38	6.07	274.28	5.61
Ecuador	ECU	3.03	-0.30	70.63	6.00	89.93	10.67	3.48	89.07	4.49

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Egypt	EGY	-0.14	-0.45	-1.05	-4.36	2.95	0.45	3.06	9.10	2.21
El Salvador	SLV	24.67	9.33	9.33	1.00	37.00	11.33	0.16	331.99	5.81
Equatorial										
Guinea	GNQ	3.50	1.50	95.75	10.50	118.00	18.25	0.00	3.01	1.10
Eritrea	ERI	2.09	0.64	-4.36	-6.64	12.36	2.00	0.72	1.73	0.55
Estonia	EST	2.14	1.14	35.43	7.14	47.71	16.57	6.35	373.66	5.92
Ethiopia	ETH	8.69	2.77	18.31	-1.08	41.66	7.47	6.51	5.89	1.77
Fiji	FJI	-0.33	-2.22	10.22	5.56	11.89	6.78	2.03	468.00	6.15
Finland	FIN	0.03	0.03	11.06	2.68	14.21	5.59	3.62	111.44	4.71
France	FRA	0.15	0.10	5.95	1.10	7.93	2.56	-0.74	866.06	6.76
French Guiana	GUF	0.14	0.00	171.71	13.00	205.57	21.14	NA	NA	NA
Gabon	GAB	1.42	0.38	118.00	13.25	142.92	22.13	-0.14	20.27	3.01
Georgia	GEO	5.00	2.63	5.38	-0.25	14.63	4.88	1.08	75.33	4.32
Germany	DEU	0.17	0.07	6.90	1.28	9.28	3.10	-5.55	288.12	5.66
Ghana	GHA	10.91	1.55	33.82	1.50	59.14	8.18	4.27	48.05	3.87
Greece	GRC	-0.90	-3.31	0.38	-0.10	0.00	-3.07	3.05	21.68	3.08
Greenland	GRL	0.00	0.00	0.00	0.00	0.00	0.00	0	NA	NA
									2991.4	
Grenada	GRD	7.00	8.00	5.00	2.00	13.00	12.00	3.31	3	8.00
Guatemala	GTM	11.00	1.18	47.91	4.45	70.64	9.45	3.65	290.90	5.67
Guinea	GIN	7.95	2.55	76.95	7.27	106.18	17.91	4.57	16.61	2.81
Guinea-Bissau	GNB	11.50	4.25	48.75	5.75	74.75	17.00	2.44	68.55	4.23
Guyana	GUY	-0.32	-0.41	149.32	11.09	182.36	19.05	2.45	3.59	1.28
Haiti	HTI	14.60	10.80	2.40	0.40	18.40	12.00	1.50	29.87	3.40
Honduras	HND	5.47	0.67	54.93	5.00	75.87	11.07	4.09	129.48	4.86
Hungary	HUN	0.14	-3.86	10.43	1.86	13.86	0.29	-4.75	459.57	6.13
Iceland	ISL	0.00	0.00	0.00	-0.11	0.02	0.02	1.26	272.04	5.61
India	IND	11.46	3.39	5.57	0.32	20.04	5.19	3.32	38.03	3.64
Indonesia	IDN	-1.13	-3.18	26.92	3.61	31.80	3.07	3.94	16.16	2.78
Iran	IRN	3.31	1.66	-1.78	-6.11	9.38	2.95	4.56	8.26	2.11
Iraq	IRQ	3.40	2.63	-2.31	-8.34	9.31	4.11	7.73	0.00	-8.38
Ireland	IRL	0.50	0.50	-1.92	-5.75	4.50	1.75	0.37	16.63	2.81
Israel	ISR	1.00	-1.75	-1.25	-2.75	4.75	-1.00	0.00	859.63	6.76

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Italy	ITA	-0.78	-2.67	0.98	-0.11	1.00	-2.22	-0.11	18.13	2.90
Ivory Coast	CIV	20.66	6.03	60.45	5.45	97.66	17.10	0.88	15.72	2.75
Jamaica	JAM	0.00	0.00	15.20	3.60	18.40	6.20	5.19	239.17	5.48
Japan	JPN	0.07	-0.36	7.41	1.70	9.41	2.87	-1.16	0	0
Jordan	JOR	-0.13	-0.25	-3.25	-10.00	8.75	1.63	2.16	31.05	3.44
Kazakhstan	KAZ	0.95	0.06	-1.01	-6.58	9.51	2.23	4.38	1.48	0.40
Kenya	KEN	10.57	2.27	15.18	-4.31	52.78	6.80	3.70	67.09	4.21
Korea, Republic of	KOR	0.47	0.33	5.07	1.27	7.20	2.93	-0.16	847.50	6.74
Kuwait	KWT	0.00	0.00	-3.50	-9.00	10.50	1.50	2.10	0	0
Kyrgyzstan	KGZ	1.67	0.86	-1.33	-3.48	6.19	1.81	4.76	1.64	0.50
Laos	LAO	1.71	0.00	22.12	1.59	30.53	3.53	2.95	13.81	2.63
Latvia	LVA	6.50	4.38	26.13	5.25	39.50	15.13	3.14	49.72	3.91
Lebanon	LBN	-2.00	-4.00	0.00	0.00	-1.00	-4.00	5.70	43.78	3.78
Lesotho	LSO	5.00	2.00	-2.33	-2.67	9.67	2.00	2.74	63.89	4.16
Liberia	LBR	6.18	1.73	120.09	12.73	152.27	23.82	3.45	7.15	1.97
Libya	LBY	0.38	0.36	-0.89	-6.82	3.01	1.71	0.00	0.02	-4.09
Lithuania	LTU	11.00	7.60	15.40	2.80	30.60	14.20	2.01	61.53	4.12
Macedonia	MKD	7.00	4.00	4.00	-0.50	14.50	5.50	-3.17	51.14	3.93
Madagascar	MDG	3.69	2.17	17.53	-0.84	32.87	10.66	0.00	37.89	3.63
Malawi	MWI	19.33	5.08	63.83	4.50	102.83	15.17	4.31	46.59	3.84
Malaysia	MYS	-3.19	-4.13	31.55	2.81	34.91	0.62	2.43	28.21	3.34
Mali	MLI	2.07	0.86	-1.49	-5.96	9.39	2.22	12.03	2.69	0.99
									2879.3	
Malta	MLT	1.00	1.00	0.00	0.00	1.00	1.00	0.87	1	7.97
Mauritania	MRT	0.14	0.07	-0.97	-3.93	3.09	0.97	2.16	1.47	0.39
									2582.3	
Mauritius	MUS	0.00	0.00	0.00	0.00	0.00	0.00	2.54	3	7.86
Mexico	MEX	3.80	0.45	13.32	-0.71	27.58	4.01	0.87	48.06	3.87
Moldova	MDA	16.50	10.50	3.00	0.50	20.50	11.50	5.65	12.05	2.49
Mongolia	MNG	0.27	0.16	-1.15	-4.78	4.73	1.27	5.39	2.45	0.90
Montenegro	MNE	4.00	2.00	3.00	0.00	8.00	3.00	2.48	0.14	-1.93
Morocco	MAR	7.35	4.58	-0.98	-3.50	12.18	5.47	8.48	6.45	1.86

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Mozambique	MOZ	5.76	2.15	77.93	7.83	106.69	18.96	3.67	16.90	2.83
Namibia	NAM	0.61	0.24	-1.17	-2.59	6.25	0.89	2.36	38.03	3.64
Nepal	NPL	16.00	3.78	1.85	0.08	19.22	4.20	3.05	87.93	4.48
									27368.	
Netherlands	NLD	0.43	0.14	-0.29	-1.71	3.43	1.00	0.43	63	10.22
New Zealand	NZL	0.00	-0.03	5.61	-0.11	9.50	5.11	2.57	668.16	6.50
Nicaragua	NIC	19.16	3.86	53.56	3.95	87.79	12.03	1.32	42.52	3.75
Niger	NER	2.61	1.24	-1.02	-6.04	8.16	2.66	3.54	5.72	1.74
Nigeria	NGA	22.31	7.45	19.95	1.36	49.47	11.45	4.85	21.04	3.05
Norway	NOR	0.29	0.29	1.04	0.08	1.85	0.92	2.83	324.80	5.78
Oman	OMN	0.01	0.00	-1.56	-5.48	4.13	1.07	1.44	0.17	-1.80
Pakistan	PAK	4.44	-0.11	-0.74	-1.77	6.22	0.25	2.40	6.77	1.91
Panama	PAN	5.87	1.20	76.27	5.80	101.47	12.07	-2.66	237.10	5.47
Papua New Guinea	PNG	0.41	0.11	39.93	7.00	48.80	11.91	0.00	14.69	2.69
Paraguay	PRY	-1.16	-2.13	65.00	5.81	85.90	12.19	8.40	8.38	2.13
Peru	PER	1.47	0.40	94.92	6.40	115.65	11.42	3.11	17.22	2.85
Philippines	PHL	9.96	3.86	15.89	2.81	29.50	8.66	1.12	72.29	4.28
Poland	POL	9.97	6.83	11.31	2.52	24.14	11.52	4.44	129.52	4.86
Portugal	PRT	3.50	2.00	4.11	-0.06	10.56	4.06	0.06	777.83	6.66
Puerto Rico	PRI	2.00	1.20	13.00	3.20	17.60	6.80	NA	NA	NA
Qatar	QAT	0.00	0.00	-1.50	-6.00	4.00	1.50	3.69	31.71	3.46
Romania	ROM	8.86	5.33	8.57	1.33	20.05	8.52	4.54	7.68	2.04
Russia	RUS	1.83	1.24	9.02	1.90	13.58	5.49	1.50	4.52	1.51
Rwanda	RWA	51.00	10.50	24.50	1.50	82.50	13.50	5.42	456.88	6.12
Saudi Arabia	SAU	0.03	0.00	-1.79	-9.72	4.96	1.79	1.08	24.50	3.20
Senegal	SEN	6.80	1.05	14.75	-1.85	36.45	5.50	2.97	39.86	3.69
Sierra Leone	SLE	21.88	6.38	55.38	5.00	91.25	15.88	4.17	9.44	2.24
Slovakia	SVK	5.75	3.00	9.75	1.75	17.75	6.50	4.28	176.39	5.17
Slovenia	SVN	0.50	0.00	19.00	3.50	26.00	6.50	-2.68	157.88	5.06
Solomon Islands	SLB	0.14	0.05	14.48	5.05	17.81	8.48	0.00	2.41	0.88
Somalia	SOM	1.13	0.58	-0.27	-2.49	4.87	1.25	NA	NA	NA
South Africa	ZAF	3.40	0.33	7.83	-0.88	18.77	2.42	0.25	91.00	4.51

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Spain	ESP	-1.47	-4.82	1.55	-0.23	1.23	-4.02	1.69	16.00	2.77
Sri Lanka	LKA	0.08	-3.54	27.38	3.77	34.54	3.77	4.39	161.45	5.08
St. Kitts and Nevis	KNA	4.00	6.00	14.00	7.00	21.00	17.00	0.04	750.00	6.62
									2401.5	
St. Lucia	LCA	7.00	9.00	9.00	4.00	17.00	15.00	-5.78	6	7.78
St. Vincent and the Grenadines	VCT	5.00	6.00	1.00	0.00	7.00	7.00	0.76	185.29	5.22
Sudan, Administered by Kenya	SDN	2.72	1.24	7.47	-7.27	25.11	5.23	2.63	1.21	0.19
Suriname	SUR	0.29	0.00	181.50	14.57	219.36	24.07	6.94	17.04	2.84
Swaziland	SWZ	10.00	2.00	68.00	4.00	103.00	14.00	2.22	55.35	4.01
Sweden	SWE	0.36	0.29	11.46	2.93	14.88	6.08	-1.66	305.79	5.72
									6237.9	
Switzerland	CHE	0.25	0.00	6.25	0.50	9.50	2.50	-0.78	4	8.74
Syria	SYR	4.11	1.89	-1.83	-6.28	9.44	3.22	0.00	3.52	1.26
Tajikistan	TJK	0.59	0.37	-0.81	-1.85	2.81	1.00	9.12	17.52	2.86
Tanzania, United Republic of	TZA	14.83	4.09	69.87	5.56	107.00	16.60	3.54	32.55	3.48
Thailand	THA	4.14	-1.20	14.74	0.90	24.76	1.58	1.87	134.37	4.90
Togo	TGO	24.60	8.00	26.00	1.00	62.60	13.40	-1.98	9.77	2.28
Trinidad and Tobago	TTO	2.75	0.75	65.75	7.25	84.00	14.25	-2.54	344.11	5.84
Tunisia	TUN	6.90	4.45	-1.05	-5.35	12.75	5.80	2.46	59.82	4.09
Turkey	TUR	8.89	4.88	1.70	-0.26	12.25	5.88	3.71	21.14	3.05
Turkmenistan	TKM	0.71	0.47	-3.12	-9.17	9.64	2.29	0.00	0.51	-0.68
Uganda	UGA	36.05	8.43	35.86	2.00	84.10	13.81	2.37	101.12	4.62
Ukraine	UKR	15.11	10.18	4.51	0.80	20.96	12.11	5.16	60.32	4.10
United Arab Emirates	ARE	0.00	0.00	-3.11	-10.54	9.04	1.93	-3.31	0	0
									2681.6	
United Kingdom	GBR	0.27	0.31	0.07	-1.87	3.07	1.49	-0.46	0	7.89
United States	USA	-1.02	-2.60	12.85	1.68	16.52	1.96	3.87	789.72	6.67
Uruguay	URY	4.29	1.82	-6.82	-8.53	15.76	3.12	3.26	37.95	3.64

## Chapter IV

Uzbekistan	UZB	1.80	1.25	-1.66	-5.20	7.23	2.36	6.58	1.27	0.24
Vanuatu	VUT	2.15	3.23	11.85	5.46	17.00	14.00	3.71	21.53	3.07
Venezuela	VEN	0.84	-0.08	69.85	3.38	96.80	10.78	0.28	26.65	3.28
Vietnam	VNM	-0.75	-3.25	9.13	0.71	11.23	-1.58	2.44	78.72	4.37
Western Samoa	WSM	0.00	0.00	0.00	0.00	0.00	0.00	-4.11	120.07	4.79
Yemen	YEM	0.45	0.43	-1.61	-7.35	5.16	1.84	0.00	1.89	0.64
Zambia	ZMB	2.84	0.77	105.16	7.61	141.95	19.23	1.08	22.80	3.13
Zimbabwe	ZWE	11.00	3.22	29.66	-1.78	67.09	10.25	7.18	NA	NA



Table SI IV-6: Species richness (SR loss) combined with z-scores of agricultural growth (World Bank Group, 2013) and spending/km<sup>2</sup> (Waldron *et al.*, 2013) for each of the three pathways. \*Countries are ranked by species loss in the Both (Intensification + expansion) pathway + agricultural growth (fifth column).

Country	Country code	Species loss + Agricultural growth (Z-scores)			Species loss - Spending/ km2 (Z- Scores)			Position in Waldron's top 40 underfunded countries
		Intensification: SR loss + Agricultural growth	Expansion: SR loss + Agricultural growth	Both: SR loss + Agricultural growth*	Intensification: SR loss - Spending	Expansion: SR loss - Spending	Both: SR loss - Spending	
Suriname	SUR	1.06	5.93	5.66	-0.93	3.94	3.68	
Congo, Rep.	COG	0.52	3.79	3.60	-1.62	1.65	1.45	18
Guyana	GUY	-0.56	3.51	3.30	-1.63	2.44	2.23	5
Paraguay	PRY	1.38	3.27	3.21	-1.40	0.49	0.44	
Liberia	LBR	0.62	3.06	2.98	-0.51	1.92	1.84	
		-1.34	3.28	2.97	NA	NA	NA	
	GUF							
		-0.09	3.01	2.83	-1.37	1.73	1.55	
	ZAR							
Mali	MLI	3.04	2.71	2.77	-1.44	-1.77	-1.71	
Cameroon	CMR	0.73	2.74	2.67	0.10	2.10	2.03	
Belize	BLZ	-0.23	2.51	2.38	-0.13	2.62	2.48	
Zimbabwe	ZWE	2.53	1.89	2.38	NA	NA	NA	
Guinea	GIN	1.24	2.27	2.35	0.06	1.09	1.16	
Malawi	MWI	2.62	1.83	2.18	1.94	1.15	1.50	
Algeria	DZA	2.42	2.24	2.14	-1.72	-1.90	-2.00	10
Brazil	BRA	-0.47	2.22	2.13	-0.93	1.75	1.67	
Rwanda	RWA	7.09	1.14	2.12	6.95	1.00	1.97	
Bolivia	BOL	0.03	2.12	2.09	-0.52	1.58	1.55	

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Peru	PER	-0.10	2.26	2.05	-0.77	1.59	1.39	
Mozambique	MOZ	0.64	1.99	2.05	-0.22	1.13	1.18	
Tanzania	TZA	1.77	1.73	2.01	1.21	1.17	1.45	
Afghanistan	AFG	2.48	1.95	1.95	-0.93	-1.46	-1.46	
Zambia	ZMB	-0.62	1.84	1.94	-0.48	1.98	2.08	
Sierra Leone	SLE	2.90	1.55	1.88	1.63	0.28	0.61	
Colombia	COL	-0.57	1.75	1.72	-0.40	1.93	1.89	27
Estonia	EST	1.10	1.76	1.67	0.56	1.21	1.12	
Tajikistan	TJK	1.85	1.73	1.62	-0.87	-1.00	-1.10	
Ecuador	ECU	0.23	1.73	1.61	0.09	1.59	1.48	
Morocco	MAR	2.50	1.50	1.61	-0.40	-1.41	-1.30	15
Ethiopia	ETH	2.00	1.35	1.58	-0.27	-0.92	-0.68	
Gabon	GAB	-1.23	1.77	1.54	-0.71	2.29	2.06	
Honduras	HND	0.75	1.51	1.51	0.56	1.32	1.32	
Swaziland	SWZ	0.69	1.22	1.47	0.80	1.33	1.58	
Iraq	IRQ	1.73	1.21	1.29	-5.03	-5.56	-5.47	1
Guatemala	GTM	1.32	1.17	1.24	1.60	1.45	1.53	
Ghana	GHA	1.52	1.00	1.20	0.86	0.35	0.55	
Cambodia	KHM	1.65	1.02	1.20	0.97	0.34	0.52	
Nigeria	NGA	3.19	0.82	1.19	2.01	-0.36	0.00	
Burundi	BDI	5.76	0.28	1.12	5.55	0.07	0.91	
Dominican Republic	DOM	1.87	1.09	1.11	1.30	0.52	0.54	
Uganda	UGA	4.11	0.40	1.10	4.41	0.70	1.40	
Equatorial Guinea	GNQ	-0.91	1.21	1.04	-1.21	0.92	0.74	
Guinea- Bissau	GNB	0.96	0.78	0.92	1.08	0.90	1.04	
Cote d'Ivoire	CIV	1.61	0.56	0.89	1.67	0.62	0.95	

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Kenya	KEN	1.28	0.30	0.87	0.95	-0.03	0.54	
Benin	BEN	1.91	0.49	0.85	1.90	0.48	0.84	
Uzbekistan	UZB	1.13	0.83	0.85	-1.78	-2.08	-2.06	14
Nicaragua	NIC	1.57	0.52	0.82	1.88	0.83	1.13	
Moldova	MDA	2.71	0.64	0.82	1.03	-1.05	-0.86	30
Brunei		-0.69	1.00	0.78	0.63	2.32	2.10	
Darussalam	BRN							
Costa Rica	CRI	-0.90	0.89	0.72	0.30	2.09	1.91	
Sri Lanka	LKA	0.16	0.87	0.70	-0.05	0.66	0.49	37
Ukraine	UKR	2.37	0.51	0.66	1.50	-0.36	-0.20	
Venezuela, RB	VEN	-1.16	0.61	0.66	-0.67	1.09	1.15	28
Jamaica	JAM	0.42	0.81	0.62	0.10	0.49	0.29	
Angola	AGO	-1.15	0.50	0.53	-3.11	-1.46	-1.42	3
Poland	POL	1.45	0.45	0.49	1.14	0.13	0.17	
Indonesia	IDN	-0.15	0.70	0.48	-1.13	-0.28	-0.49	31
Romania	ROM	1.35	0.41	0.43	-0.14	-1.08	-1.05	
Mongolia	MNG	0.53	0.43	0.38	-1.71	-1.80	-1.85	25
Latvia	LVA	0.56	0.40	0.38	0.31	0.15	0.13	
Lebanon	LBN	0.34	0.57	0.36	-0.84	-0.61	-0.82	
Slovak Republic	SVK	0.85	0.35	0.29	0.72	0.22	0.16	
Senegal	SEN	0.54	0.04	0.26	0.26	-0.25	-0.03	11
Australia	AUS	0.10	0.28	0.21	-0.42	-0.24	-0.31	38
Iran, Islamic Rep.	IRN	0.63	0.13	0.20	-0.83	-1.33	-1.26	
Armenia	ARM	1.38	0.04	0.20	0.95	-0.39	-0.23	29
Kyrgyz Republic	KGZ	0.49	0.21	0.20	-1.69	-1.96	-1.98	

Chapter IV

Cuba	CUB	1.10	0.10	0.19	0.87	-0.12	-0.03	
Bangladesh	BGD	0.12	0.30	0.17	-0.31	-0.14	-0.26	
Belarus	BLR	0.49	0.13	0.17	-0.74	-1.11	-1.07	
Kazakhstan	KAZ	0.27	0.09	0.14	-1.82	-2.00	-1.94	
United States	USA	-0.16	0.29	0.12	0.45	0.90	0.73	
Lao PDR	LAO	-0.12	0.23	0.12	-0.83	-0.47	-0.58	
Azerbaijan	AZE	0.95	-0.01	0.11	-0.05	-1.01	-0.89	33
Vanuatu	VUT	0.19	0.21	0.08	-0.59	-0.57	-0.70	13
Albania	ALB	1.01	0.06	0.07	0.89	-0.06	-0.05	
Malaysia	MYS	-0.94	0.31	0.04	-1.17	0.07	-0.20	7
India	IND	1.26	-0.09	0.01	0.84	-0.51	-0.41	
Finland	FIN	-0.11	0.16	-0.01	-0.20	0.07	-0.11	17
Turkey	TUR	1.07	-0.06	-0.03	0.27	-0.86	-0.82	
China	CHN	0.00	0.07	-0.10	-1.07	-0.99	-1.16	39
Nepal	NPL	1.76	-0.29	-0.10	1.76	-0.28	-0.09	
Uruguay	URY	0.32	-0.45	-0.10	-0.09	-0.85	-0.50	
Sudan	SDN	-0.10	-0.28	-0.11	-1.67	-1.85	-1.68	34
Grenada	GRD	0.68	-0.11	-0.15	2.02	1.22	1.19	
Niger	NER	0.19	-0.20	-0.18	-1.06	-1.45	-1.43	
Lithuania	LTU	0.75	-0.28	-0.21	0.98	-0.05	0.02	
Burkina Faso	BFA	0.72	-0.74	-0.21	0.51	-0.95	-0.42	
Qatar	QAT	-0.09	-0.16	-0.22	-0.71	-0.78	-0.84	
Chad	TCD	-0.07	-0.31	-0.23	-1.43	-1.66	-1.58	
Panama	PAN	-1.51	-0.23	-0.24	0.85	2.14	2.13	
Canada	CAN	-0.38	-0.19	-0.37	-0.24	-0.05	-0.23	
Thailand	THA	-0.18	-0.34	-0.38	0.40	0.24	0.20	
Lesotho	LSO	0.23	-0.51	-0.42	0.21	-0.52	-0.43	

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Antigua and Barbuda	ATG	-0.08	-0.35	-0.43	1.86	1.60	1.51	
Tunisia	TUN	0.38	-0.57	-0.45	0.43	-0.51	-0.39	
Egypt, Arab Rep.	EGY	-0.33	-0.36	-0.46	-1.23	-1.27	-1.36	
New Zealand	NZL	-0.48	-0.35	-0.48	0.51	0.64	0.51	
Vietnam	VNM	-0.62	-0.30	-0.49	-0.44	-0.13	-0.31	
Papua New Guinea	PNG	-1.31	-0.30	-0.49	-0.97	0.04	-0.16	
Greece	GRC	-0.43	-0.33	-0.53	-0.98	-0.88	-1.08	
Bhutan	BTN	0.00	-0.44	-0.53	0.38	-0.06	-0.14	23
Philippines	PHL	0.31	-0.57	-0.53	0.91	0.02	0.06	
Montenegro	MNE	0.01	-0.45	-0.54	-2.36	-2.82	-2.91	
Dominica	DMA	-0.33	-0.40	-0.56	1.27	1.20	1.04	
Norway	NOR	-0.35	-0.39	-0.56	0.26	0.22	0.05	
Trinidad and Tobago	TTO	-1.88	-0.47	-0.59	0.60	2.00	1.89	12
Pakistan	PAK	0.04	-0.58	-0.61	-0.76	-1.38	-1.41	
Fiji	FJI	-0.71	-0.41	-0.61	0.33	0.62	0.42	
Kuwait	KWT	-0.64	-0.76	-0.62	-2.10	-2.22	-2.08	
Namibia	NAM	-0.47	-0.61	-0.62	-0.56	-0.70	-0.71	
Jordan	JOR	-0.63	-0.73	-0.64	-0.74	-0.84	-0.74	32
Haiti	HTI	1.04	-0.80	-0.65	1.15	-0.70	-0.54	
Argentina	ARG	-0.86	-0.56	-0.65	-1.11	-0.81	-0.90	
Mexico	MEX	-0.57	-0.73	-0.66	-0.05	-0.21	-0.15	
Mauritius	MUS	-0.49	-0.51	-0.70	1.05	1.03	0.84	
El Salvador	SLV	1.88	-1.08	-0.70	3.42	0.46	0.84	
Russian Federation	RUS	-0.61	-0.63	-0.76	-1.26	-1.28	-1.41	

## Chapter IV

Central African Republic	CAF	-3.09	-0.65	-0.76	-0.93	1.51	1.40	
Mauritania	MRT	-0.60	-0.67	-0.76	-1.93	-2.00	-2.09	22
		-0.83	-0.59	-0.78	0.06	0.30	0.12	
	CZE							
Denmark	DNK	-0.68	-0.63	-0.80	0.00	0.05	-0.12	
Madagascar	MDG	-0.89	-0.91	-0.85	-0.17	-0.19	-0.13	
Togo	TGO	1.14	-1.36	-0.87	1.99	-0.51	-0.01	
Georgia	GEO	-0.34	-0.87	-0.88	0.28	-0.24	-0.25	
Comoros	COM	-0.20	-0.79	-0.88	-0.17	-0.77	-0.86	20
Myanmar	MMR	-0.94	-0.80	-0.89	-1.62	-1.48	-1.57	
Botswana	BWA	-0.97	-0.99	-0.89	-0.72	-0.74	-0.63	35
Spain	ESP	-0.97	-0.76	-0.96	-1.18	-0.97	-1.17	
Cyprus	CYP	-0.86	-0.79	-0.97	0.10	0.17	-0.01	
Oman	OMN	-0.86	-0.93	-0.99	-2.82	-2.89	-2.95	
Eritrea	ERI	-0.84	-1.26	-1.05	-1.61	-2.03	-1.82	8
South Africa	ZAF	-0.84	-1.09	-1.07	0.15	-0.10	-0.09	
		-0.83	-0.99	-1.09	1.07	0.91	0.81	
	KNA							
Saudi Arabia	SAU	-0.99	-1.06	-1.09	-0.81	-0.89	-0.92	
Iceland	ISL	-0.93	-0.95	-1.14	0.15	0.12	-0.06	26
		-0.45	-1.10	-1.15	0.64	0.00	-0.06	
	VCT							
Chile	CHL	-0.99	-1.01	-1.16	-0.77	-0.79	-0.95	9
		-1.34	-0.99	-1.18	-1.73	-1.38	-1.57	6
	SLB							
Puerto Rico	PRI	-1.10	-1.03	-1.18	NA	NA	NA	

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Bosnia and Herzegovina	BIH	-0.31	-1.26	-1.23	0.46	-0.50	-0.46	
Malta	MLT	-0.93	-1.09	-1.25	1.23	1.07	0.91	
Djibouti	DJI	-1.36	-1.50	-1.29	-3.05	-3.20	-2.99	2
Portugal	PRT	-0.89	-1.25	-1.32	1.02	0.66	0.59	
Ireland	IRL	-1.17	-1.31	-1.35	-0.91	-1.05	-1.09	
Netherlands	NLD	-1.16	-1.25	-1.35	2.06	1.97	1.87	
Barbados	BRB	-0.33	-1.36	-1.35	1.42	0.38	0.39	
Turkmenistan	TKM	-1.27	-1.47	-1.36	-2.28	-2.48	-2.37	
		-0.83	-1.44	-1.36	-1.06	-1.67	-1.60	
	SYR							
Yemen, Rep.	YEM	-1.30	-1.43	-1.46	-1.79	-1.92	-1.94	
Somalia	SOM	-1.21	-1.39	-1.46	-1.96	-2.13	-2.21	
Israel	ISR	-1.23	-1.42	-1.47	0.74	0.55	0.51	
Korea, Rep.	KOR	-1.35	-1.30	-1.47	0.67	0.72	0.55	
Libya	LBY	-1.31	-1.41	-1.51	-3.70	-3.80	-3.89	
Greenland	GRL	-1.36	-1.39	-1.57	NA	NA	NA	
Italy	ITA	-1.50	-1.40	-1.59	-1.04	-0.94	-1.13	
Switzerland	CHE	-1.60	-1.48	-1.63	1.44	1.55	1.41	
France	FRA	-1.59	-1.48	-1.65	0.64	0.75	0.58	36
		-1.48	-1.54	-1.66	1.10	1.05	0.93	
	GBR							
Japan	JPN	-1.75	-1.58	-1.76	-2.09	-1.93	-2.11	
		-2.70	-1.59	-1.77	-0.23	0.88	0.70	
	BHS							
Sweden	SWE	-1.88	-1.64	-1.81	0.24	0.48	0.31	
Austria	AUT	-1.84	-1.72	-1.88	0.79	0.91	0.75	40
Slovenia	SVN	-2.22	-1.79	-1.92	0.00	0.42	0.29	16
Belgium	BEL	-2.23	-1.97	-2.13	1.29	1.55	1.39	

Chapter IV

Macedonia, FYR	MKD	-1.54	-2.37	-2.34	0.38	-0.44	-0.41
United Arab Emirates	ARE	-2.50	-2.61	-2.51	-2.10	-2.21	-2.11
Bulgaria	BGR	-1.30	-2.72	-2.64	0.95	-0.47	-0.39
Hungary	HUN	-2.97	-2.74	-2.90	0.38	0.62	0.46
Samoa	WSM	-2.77	-2.80	-2.98	-0.18	-0.20	-0.39
Croatia	HRV	-2.84	-3.01	-3.04	0.64	0.47	0.43
St. Lucia	LCA	-2.44	-3.13	-3.18	1.93	1.24	1.19
Germany	DEU	-3.24	-3.10	-3.27	0.20	0.34	0.17







## **Chapter V: Synthesis**

## 1 Summary and main conclusions

The overarching goal of this thesis was to advance scientific understanding of the relationship between agricultural land use and biodiversity. This thesis employed a variety of approaches to address this goal. First, by providing improved knowledge about the spatial concordance of the many facets of land-use intensity and biodiversity and thus highlighting the multidimensionality of land-use intensity along with regions that could pose a threat to biodiversity. Second, this work sheds new light on novel aspects of species-area relationships at a global scale, showing that land-use intensity indicators rival biomes in predicting broad scale patterns of species richness. Finally, important advances were made in assessing the biodiversity impact of alternative future agricultural developmental pathways. The insights gained from this research answer the three core research questions of this thesis.

*Research Question I: How do patterns of land-use intensity relate to patterns of biodiversity?*

Chapter II provided answers to this question by introducing a global view of the geographic patterns of land-use intensity. Many regions were highlighted where highly intensive agriculture and unique biodiversity coincide. Areas where high land-use intensity may pose a threat to biodiversity were found predominantly in Sub-Saharan Africa, the tropical Andes, and South-East Asia. Results suggest that individual land-use intensity metrics highlight different high-pressure regions, suggesting that the choice of intensity metric is important when considering conservation threat. This chapter shows that conservation research should include multiple intensity metrics when considering biodiversity threat. By not doing so, the full spectrum of land-use intensity's threat to biodiversity may be underestimated.

*Research Question II: To what extent does the inclusion of land cover and land-use intensity improve global SAR models?*

Chapter III systematically compared SARs by accounting for geographic variation in biomes, land cover and a range of land-use intensity indicators. Land-use intensity was found to perform as well as biomes in predicting species richness, but only in terms of percentage HANPP - a system level metric. Other land-use intensity metrics, for instance, fertiliser, cereal yields, or irrigation did not perform as well. This shows for the first time that broad agricultural factors can rival environmental factors in predicting global species richness. This chapter suggests that the inclusion of land-use intensity in SAR models allow for better predictions and thus a deeper understanding of global biodiversity patterns.

*Research Question III: How may future pathways of agricultural expansion and intensification threaten biodiversity?*

Chapter IV highlighted particularly high-risk areas in terms of biodiversity loss due to agricultural expansion and intensification. Expansion risk areas were found across the Amazon and Sub-Saharan Africa. Whereas intensification risk-areas were mainly in India, Eastern Europe, and the Afrotropical, and African Great lakes region. The single most at risk area in terms of species loss was found in the Peruvian Amazon and is currently only partially within the borders of IUCN category protected areas. On a national-level, Sub-Saharan African and Latin American countries dominated the top ten ranks, particularly Suriname, French Guiana, and Guyana, in terms of species loss, and the DRC and Rep. of Congo, in terms of losses of abundance. Highlighting potential future areas where biodiversity is most at risk is a great challenge for science today, and this chapter is among the first to directly address the spatial composition of future land-use pathways on biodiversity. The results from this work provide novel insights into this globally pressing issue and thus help identify areas, most notably in Sub-Saharan Africa and the Amazon, most at risk in terms of potentially conflicting agricultural development and biodiversity conservation goals.

## **2 Cross-cutting insights**

The results from each core research chapter provide responses to the three research questions of this thesis. Based on these results, three crosscutting insights emerged that address the overarching goal of this thesis: gaining a deeper understanding of the relationship between agricultural land use and biodiversity.

First, the importance of land-use intensity in the nexus of land use and biodiversity research was emphasised. The many dimensions of land-use intensity concordant with biodiversity were presented in Chapter II, the importance of land-use intensity in predicting species richness was illustrated in Chapter III, and finally the spatially explicit impact of potential pathways of intensification was highlighted in Chapter IV. This thesis showed that land-use intensity should not be treated as synonymous to yields, or indeed any one single metric. This was found to be the case both in terms of patterns, where different intensity metrics can result in a spatially explicit multitude of threats to biodiversity (Chapter II) and predictive ability, where a large difference was shown in the ability of various intensity metrics to predict global patterns of species richness (Chapter III). Moreover, all

three core research chapters exemplified the many ways in which land-use intensity is a crucial part of conservation research, in its multidimensionality, its predictive ability, and its potential risk to biodiversity. In general, the land use and conservation communities have not fully embraced either the complexity nor the importance of land-use intensity. This thesis made progress in shedding light on this issue and bridging this gap.

Second, the approach taken in Chapter II and IV, where biodiverse areas at risk of agricultural land use were highlighted, allows for a different perspective on the nexus of agriculture and conservation. Such issues have generally been framed as a choice between land-sparing and land-sharing. Importantly, this thesis shows that there are other worthwhile ways to approach this complex topic. By instead illustrating the spatial patterns of land-use intensity concordant with biodiversity (Chapter II), and then highlighting the areas potentially most at risk to either expansion or intensification (Chapter II & IV), this thesis moves outside the land-sparing/land-sharing framework and presents an alternative context by which to prioritise actions. Therefore, instead of asking what hypothetical approach might be least harmful to biodiversity, this thesis instead highlights where and how biodiversity may be under threat, both now and in the future. This approach acknowledges the fact that while agriculture should not be seen as the antithesis of the natural world (Perfecto & Vandermeer, 2010), current widespread industrial techniques are harmful to biodiversity (Newbold *et al.*, 2015) and therefore the threats they pose must be identified. Considering that these threats are expected to escalate in the future (Lambin & Meyfroidt, 2011), the approach adopted in Chapter II and IV allows for a straightforward way in which to plan for the future by identifying regions potentially at risk. While Chapter II achieved this through mapping current levels of intensity and thus the potential for intensification, Chapter IV took a step further by creating pathways of agricultural development. Both approaches are useful, the strength in Chapter II lies in a particularly nuanced view of the many facets of threat due to intensification, whereas, Chapter IV quantifies the potential future impact of agriculture on biodiversity. Timing in conservation is crucial, where well-planned proactive action, rather than reactive schemes, can improve the chances of success, take less time to implement, and make the most out of limited funds (Cook *et al.*, 2014; Oliver & Roy, 2015). Such forward looking approaches provide particularly useful spatial information in designing conservation prioritization schemes that aim to better account for future agricultural threat. All in all, highlighting at risk areas is a crucial first step in effectively pin-pointing regions most in need of conservation attention, both now and in the future.

Third and finally, this thesis made important steps in bringing the relationship between agricultural land use and biodiversity to the global scale. The issue of scale in place-based research can never be fully resolved. At each level of scale from local to regional to global, there are obvious trade-offs to what can and cannot be known. Most research that deals with human impact on natural systems focuses on local to regional scales (see Newbold *et al.*, 2015 for review). On the other hand, broader macroecological studies, that generally focus on biophysical factors, span over larger regions and often work at global scales (Hawkins *et al.*, 2003b; Hawkins *et al.*, 2003a; Field *et al.*, 2009; Hortal *et al.*, 2012). This thesis helps to bridge this gap by adding to the relatively small body of literature that has assessed the relationship between agricultural land use and biodiversity at the global scale.

A common characteristic across all three core research chapters is that they take recently available global scale datasets and combine them in novel ways in order to highlight where and how agricultural activity relates to biodiversity. This was particularly noteworthy in the case of Chapter III, where human factors have never before been shown to predict species richness on a par with natural biophysical characteristics on a global level. This is valuable information given that land use is the most important driver of *local* biodiversity patterns, yet now, land-use intensity factors can allow for better predictions and a deeper understanding of *global* biodiversity patterns. The global scale is valuable in a different way with regard to Chapter II and IV, where global scale research can highlight the areas most at risk in terms of biodiversity loss - regardless of political boundaries. This is useful since most prioritization schemes are national to regional scale. Such schemes are therefore not optimized for globally relevant biodiversity conservation and may lead to sub-par solutions (Zimmerer *et al.*, 2004). International conservation planning can lead to better returns on investment and outcomes for biodiversity than those carried out within the strict borders of nations (Dobrovolski *et al.*, 2014). Thus, in order to best develop effective conservation plans, the global perspective has a unique advantage where benefits to conservation can be weighed up and the potential for the most effective cross-boundary solutions may be found. Moreover, national to regional level planning has the potential to outsource conservation conflict to developing nations – whereby strict environmental protection at home leads to increased imports from biodiverse rich but governance-poor regions (Lambin & Meyfroidt, 2011). While potential leakage effects are outside the scope of Chapter II and IV, the results found here are not geographically constrained and therefore provide an ideal starting point in emphasising current and potential future agricultural landscapes most in need of conservation planning.

### **3 Implications for policy**

In light of the pressing need to best figure out how to produce more food with as little harm to the natural world as possible, this thesis can contribute by providing policy makers with fine-scale information on where biodiversity is at risk due to agricultural land use: both today in the case of land-use intensity, and in the future, in the case of potential for both expansion and intensification. The results of this thesis may be particularly useful in guiding global-scale conservation organisations that aim to prioritise regions most at risk under current or future land use regimes. This approach allows decision makers to target regions and develop context-specific conservation plans, either in terms of finding sustainable ways to increase production on already farmed land, or, where appropriate, protecting intact natural areas at risk of expansion.

Some results from this thesis have already been included in such global scale initiatives. For example, two programs in particular in the UNEP-WCMC have taken interest in this work. The “Commodities and biodiversity” program aims to provide decision makers with the information and tools needed to balance future demands for land along with finding ways to ease pressure on ecosystems at risk, whilst the “Supporting national biodiversity planning” program support countries in developing comprehensive National Biodiversity Strategies and Action Plans. The results from Chapter II were taken into account in terms of rethinking how to conceptualise biodiversity risk due to intensification – a broader view is now taken that includes the many facets of land-use intensity. Chapter IV can provide useful information with regard to future threats and national level planning. Results should be taken only as one piece of the puzzle, not as a framework to be directly applied. Information on transdisciplinary socio-economic dimensions at multiple scales are also necessary in combination with the results from this thesis.

### **4 Outlook**

This century will bring unprecedented environmental and societal challenges on a scale never before seen. This thesis brought an improved understanding of the complex relationship between agricultural land use and biodiversity by mapping current and future at risk areas, and showing that land-use indicators can predict broad-scale patterns of biodiversity on a par with natural biophysical factors. However, a number of interesting topics beyond the scope of this dissertation emerged during the course of this work.



Prevailing research within the nexus of food and fauna has overwhelmingly focused on agricultural production (Green *et al.*, 2005). This makes some sense when viewed from a conservationist's perspective where the direct effects of agricultural land use on biodiversity are of utmost concern. However, this viewpoint is overly narrow when packaged as an integral part of solving the broader issue of 'feeding the world'. Increased production is by no means synonymous with food security (Barrett, 2010; Tscharntke *et al.*, 2012). When thinking in terms of reducing hunger, it is small-scale farms, not large-scale industrially intensified farms, that are the backbone of food-security (Tscharntke *et al.*, 2012). Thus, caution must be taken regarding whether the increasingly popular 'feed the world' paradigm includes feeding those that demand luxury items and highly inefficient meat and dairy – often at the expense of those living in hunger (Tscharntke *et al.*, 2012; Rulli *et al.*, 2013). So far, research in this area has sent mixed messages, both in terms of what food security means and how to resolve it (Barrett, 2010; Tscharntke *et al.*, 2012). The agro-ecological approach may hold great promise in resolving this complex issue. While much of this thesis has focused on negative effects of industrial agriculture, a relatively small body of research is beginning to show that some agroecological practises can benefit biodiversity and provide competitive yields (Foley *et al.*, 2005; Tscharntke *et al.*, 2005). Encouragingly, this approach also been shown to be highly beneficial for long-term sustainability and food security, as the food produced is for direct local consumption (De Schutter, 2011). Thus, in order to better distinguish between food production and food security, a clearer differentiation between crops for direct consumption versus feed and fuel crops is needed. Better integration of spatially explicit ground based data with satellite imagery could fill this gap by verifying whether crops are destined for direct consumption or are part of a chain of livestock or biofuel production. Following this, investigating the biodiversity impacts of such food systems could hold interesting results, where synergies between landscapes that produce food for direct consumption and simultaneously support biodiversity may be found.

While this thesis took a global view, the impact of globalisation on land-use transitions and associated biodiversity change was beyond the scope of current work. How and where consumption patterns affect agricultural land use and biodiversity is a field ripe with fascinating research avenues. For example, China announced new dietary guidelines this year recommending a 50% reduction in meat consumption (Chinese Dietary Guidelines, 2016), if such a transition were to occur, what could this mean for soy feed expansion and intensification in Latin America? Or, considering Norway's recent 'ban' on all products linked to deforestation (Norwegian Rainforest Foundation, 2016), if this policy was adopted

across the EU, how could this transform tropical deforestation frontiers and associated threats to biodiversity? While recent research has shown the overall amount of land that would be saved under various global changes in diet and land use (Erb *et al.*, 2016a), spatially explicit results were not possible due to data gaps in spatial information on trade flows. Bridging such gaps would allow for the investigation of levers of change from the fundamental level of root drivers.

Improvements in both land use and biodiversity datasets are needed in order to achieve many of the above mentioned goals. First, of the available land use datasets, livestock data remains most neglected (Erb *et al.*, 2016b). No global datasets are currently available indicating areas suitable for livestock, with large data gaps remaining in assessing the extent and intensity of grazing activities (Erb *et al.*, 2016b). More worrying still, due to strict data protection, mapping current industrialised livestock units is problematic (Wint & Robinson, 2007), let alone assessing the impact of such operations on biodiversity.

Second, Chapter II and III of this thesis could not provide a causal analysis between global land use and biodiversity. This was primarily due to a lack of global time series datasets for both biodiversity and land use (particularly intensity) indicators. Developing such indicators might be possible on the biodiversity side by mining natural history museums records and databases of historical species occurrences. On the land use side, this may be possible by better integrating historical satellite- and ground-based data, along with more comprehensive incorporation of land management in Earth system models (Erb *et al.*, 2016c).

Third, the PREDICTs database gives unprecedented information on the effect of land use on biodiversity by using a space-for-time approach (Newbold *et al.*, 2015). Still, there is more contained in this data than is currently openly available. Assessing the effect of land use on biodiversity split by taxa, species traits, and threatened vs non-threatened species could hold a treasure-trove of valuable information.

Fourth and finally, much of this thesis focused on species richness. However, this metric is far from ideal: it can be over-representative of common, widespread species and can overshadow rare or small-ranged species, often most in need of conservation (Grenyer *et al.*, 2006). On top of this, species richness alone gives no indication of endemism, rarity, species turnover, phylogenetic diversity, genetic diversity, functional diversity, ecological resilience or trophic interaction. For this reason, endemism richness was used in Chapter II, thus giving a more holistic view of the importance of a grid cell for conservation. Unfortunately, using alternative metrics such as this can become difficult when later comparing to other research,

and in being able to utilise larger databases that are often based on commonly used indicators such as species richness (e.g. the PREDICTs database; Hudson *et al.*, 2014). If data collection in the field and collation in the lab included a richer set of biodiversity indicators, then our understanding of ecological effects would not be so constricted.

The way in which we conceptualise problems shapes how we come to design and implement solutions. Agriculture currently impacts the majority of the world's ecosystems (Ellis & Ramankutty, 2008) and threatened species (Maxwell *et al.*, 2016), and this impact is set to rise in the future (Sala *et al.*, 2000). Policy makers and research efforts should better reflect the importance of agriculture in conservation research and action. Within this, more careful attention should be given to the multifaceted nature of farming, specifically: a better inclusion of the many ways in which we produce crops, a more holistic view of the destination of produce in terms of food versus feed versus fuel, and a deeper understanding of the underlying levers worth pulling in order to truly reconcile food and fauna.



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## PEER-REVIEWED JOURNAL ARTICLES

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- [1] **Kehoe, L.**, Romero-Muñoz, A., Polaina, E., Estes, L., Kreft, H., and Kuemmerle, T. (2017). Biodiversity at risk under future cropland expansion and intensification. *Nature Ecology and Evolution*. doi:10.1038/s41559-017-0234-3
- [2] **Kehoe, L.**, Senf, C, Meyer, C, Gerstner, K, Kreft, H & Kuemmerle, T (2016) Agriculture rivals biomes in predicting global species richness. *Ecography*, doi:10.1111/ecog.02508
- [3] Estes, LD, Searchinger, T, Spiegel, M, Tian, D, Sichinga, S, Mwale, M, **Kehoe, L.**, et al. Reconciling agriculture, carbon, & biodiversity in a savanna transformation frontier (2016) *Proc. R. Soc. B*. doi:10.1098/rstb.2015.0316
- [4] Ritchie, E, Dorresteijn, I, Schultner, J, Nimmo, D, Hanspach, J, Kuemmerle, T, **Kehoe, L.** & Fischer, J (2016) Crying wolf: limitations of predator-prey studies need not preclude their salient messages. *Proc. R. Soc. B*. 283 (1834).
- [5] Kühl, H, Kalan, A, Arandjelovic, M, Aubert, F, D'auvergne, L, Goedmakers, A, Jones, S, **Kehoe, L.**, et al. (2016) Chimpanzee Accumulative Stone Throwing, *Nature Scientific Reports* (6), 22219.
- [6] **Kehoe, L.**, Kuemmerle, T, Meyer, C, Levers, C, Václavík, T, & Kreft, H (2015) Global Patterns of agricultural land-use intensity and vertebrate diversity. *Diversity and Distributions* 21 (11), 1308-1318.
- [7] Dorresteijn, I, Schultner, J, Ritchie, E, Nimmo, D, Hanspach, J, Kuemmerle, T, **Kehoe, L.** & Fischer, J (2015) Incorporating anthropogenic effects into trophic ecology: predator-prey interactions in a human-dominated landscape. *Proc. R. Soc. B* 282 (1814), 1602.

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## CONFERENCE CONTRIBUTIONS

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## **Eidesstattliche Erklärung**

Hiermit erkläre ich, die vorliegende Dissertation selbstständig und ohne Verwendung unerlaubter Hilfe angefertigt zu haben. Die aus fremden Quellen direkt oder indirekt übernommenen Inhalte sind als solche kenntlich gemacht. Die Dissertation wird erstmalig und nur an der Humboldt-Universität zu Berlin eingereicht. Weiterhin erkläre ich, nicht bereits einen Dokortitel im Fach Geographie zu besitzen. Die dem Verfahren zu Grunde liegende Promotionsordnung ist mir bekannt.

Laura Kehoe

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