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Genius loci ...

Landscape ecology in the Anthropocene:
Spatial aspects of human–environment interactions across scales

Habilitation Thesis

Field of Study: Ecology

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1 Introduction

1.1 Anthropocene

Humans have a profound influence on the environment, altering the Earth's ecosystems at an increasing rate (Foley et al. 2005, Newbold et al. 2015). Today, nearly all of the planetary systems have been transformed by human activities, including changes in atmospheric chemistry and global climate, alteration of ocean ecosystem functioning, and rapid transformation of terrestrial biosphere, all of which leading to unprecedented declines in global biological diversity (Ellis 2011, Steffen et al. 2011a, Ellis et al. 2012). The massive conversion of natural habitats into intensively managed land systems and anthropogenic biomes (anthromes; Figure 1) caused the emergence of novel ecological patterns and processes (Ellis 2011). The magnitude, variety and significance of human-induced changes reached such a scale that they led to the notion that we now live in a new geological era defined by the actions of humans: the Anthropocene (Zalasiewicz et al. 2011, Wigginton 2016).

The use of the term 'Anthropocene' has become quickly popular after the first influential paper was published nearly two decades ago (Crutzen 2002). Since then, the concept has been widely debated, while several scientific journals have launched focusing on this topic: e.g. The Anthropocene or Elementa (Lewis and Maslin 2015). The concept of the Anthropocene implies that the imprint of human societies on the global environment is now so large and pervasive that the Earth has left the Holocene, the environment within which complex human societies have developed (Steffen et al. 2011b). Because a marked global-scale shift in the Earth state and its signature in the geological record is what is needed to formally recognize a new geological time unit, the reason for defining Anthropocene appears justifiable. Human influence is now global, it represents the dominant force behind most current environmental change, and its impact will likely be observable in the geological stratigraphic record for thousands of years into the future (Lewis and Maslin 2015). More importantly, accepting the emergence of Anthropocene is a reminder that the Holocene has been a relatively stable and accommodating state of the Earth System and is the only environment that we know with certainty that it can support contemporary human population (Steffen et al. 2011b).

Despite the wide agreement that humans replaced nature as the dominant environmental force on Earth, there is currently no consensus on when exactly the Anthropocene started (Ellis et al. 2016, Wigginton 2016). Formal proposals for recognizing the beginning of the Anthropocene have ranged, so far, from the onset of agricultural and animal domestication, through the start of Industrial Revolution, to the Great Acceleration of population growth and natural resource use (Steffen et al. 2016). First, the 'early Anthropocene' some 8,000 years ago has been proposed as the beginning of the human-dominated era because of the marked intensification of farming activities after agriculture became widespread in many regions across the world. The advent of agriculture caused a significant global impact on Earth's ecosystems and climate due to extensive deforestation, leading to increases in species extinction rates, and changes in global biochemical cycles, leading to gradual increases in atmospheric carbon dioxide (CO₂) and methane (CH₄) levels (Lewis and Maslin 2015). Second, the beginning of the Industrial Revolution at ~1800 C.E. has been suggested as the onset date of the Anthropocene because humans began to use fossil fuel for energy that replaced biomass fuel and human and animal labor. Societies also started applying

scientific methods and technologies, which dramatically enhanced human survival rates, allowed creating new social networks (e.g. global trading system), and increased the intensity and pace of human–environment interactions (Ellis 2011). However, these activities show smooth rather than abrupt and globally synchronous change in ice core records and geological markers (Lewis and Maslin 2015). Third, the Great Acceleration of population growth, industrialization, and the use of natural resources in the mid-twentieth century appear to best fulfill the criteria of geological stratigraphic markers to signify the inception of the Anthropocene (Lewis and Maslin 2015, Ruddiman et al. 2015). This era is characterized by large changes in natural biochemical cycles and the development of new materials, including plastics, organic and inorganic pollutants, and radioactive compounds detectable in geological records.

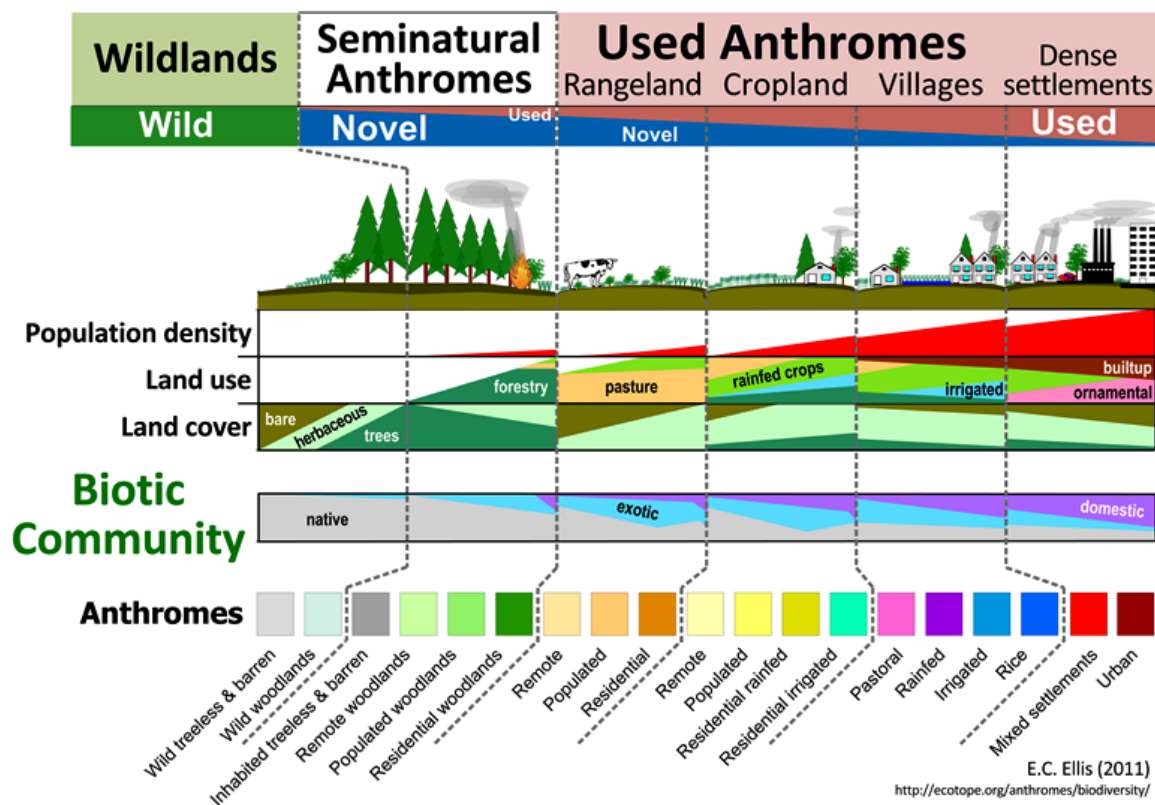


Figure 1. Global anthromes: conceptual framework for anthropogenic transformation of terrestrial biomes. Adopted from Ellis (2011).

Despite the different hypotheses on when the Anthropocene is best geologically justified, there is little doubt that the contemporary society is well in the epoch and that we may be crossing or already crossed many planetary boundaries (Foley et al. 2007, Rockström et al. 2009, Barnosky et al. 2012). This also shows that there is a pressing need to achieve effective planetary stewardship. Without it, we may risk driving the Earth System over a safe tipping point of the planetary biosphere from which we cannot easily return (Steffen et al. 2011b). All this requires that we better understand the causes and consequences of human–environment interactions. To do so, we need to study (i) how humans affect landscapes and ecosystems across a range of spatial and temporal scales, (ii) how novel ecological patterns and processes emerge and at which scales

they operate, and (iii) how understanding the human-induced alterations of the environments in the past can help us predict, mitigate and adapt to changes that we face in the future. This is the right task for the scientific discipline of Landscape Ecology.

1.2 Landscape Ecology

Landscape ecology is a scientific discipline that offers new theoretical concepts as well as methods and techniques that allow us to study the interactions between spatial patterns of landscape or ecosystem properties and a wide range of ecological processes (Turner 2005). Landscape ecology supports the development of scientific models on spatial relationships among ecological phenomena, the acquisition of new types of data on ecological patterns and dynamics, and the examination of spatial scales that are rarely addressed in typical ecological studies (Pickett and Cadenasso 1995). The term 'landscape ecology' was first coined by the German geographer Carl Troll in an attempt to integrate the 'spatial' (horizontal) approach of geographers focusing on mapping spatial patterns and the 'functional' (vertical) approach of ecologists focusing on explaining ecological processes (Cord et al. 2013). As such, landscape ecology has become a frontier of ecology and landscape management in the last decades, and is still expanding its scope, especially into the realm of ecosystem services and land system science (Verburg et al. 2015).

Landscape ecology is well positioned to deal with the challenges of the Anthropocene epoch. This is due to several specific aspects that distinguish landscape ecology from other sub-disciplines within ecology. First, landscape ecology acknowledges that everything is spatial in the Anthropocene. Unlike other sub-disciplines, landscape ecology aims at explaining ecological phenomena in the context of 'where' they are happening and what the causes and consequences of spatial heterogeneity are (Wu and Hobbs 2002, Turner 2005). No matter whether the focus is on deforestation, land abandonment, urban sprawl or large-scale land acquisition, their understanding always requires considering spatial interactions and the geographical context of those issues.

Second, landscape ecology is centered around the critical concept of scale, which refers to the spatial (or temporal) dimension of an object or a phenomenon (Levin 2011). The prominent role of scale in landscape ecology likely comes from the fact that pressing environmental issues started occurring across increasingly larger geographical areas. However, while environmental issues and their impacts may manifest even at global scales, decision making, landscape planning and conservation management typically operate at local, regional or national scales. Moreover, changing the grain (e.g. the minimal unit of analysis) or the extent of the area studied may yield different results, and seemingly contradictory findings of different studies may be sometimes attributed to the differing scales at which they were conducted (Wu and Hobbs 2002, Levin 2011). Therefore, landscape ecologists, planners and conservation practitioners often strive to find practical ways of extrapolating findings between fine and broad spatial scales.

Third, the anthropogenic activity is usually not the major component in ecological studies but it is typically the central factor investigated in landscape ecology (Turner 1989, 2005). Landscape ecology is therefore considered an interdisciplinary science that combines natural and social science disciplines with landscape architecture and regional planning to examine landscapes as the living environments for human societies. Although every organism may perceive landscapes

differently (and for small species with limited dispersal landscapes may represent areas of only square meters or centimeters), the human scale is typically applied when studying landscapes, often described from human perspective as spatially heterogeneous mosaics over which ecosystems recur across tens, hundreds or even thousands of kilometers (Forman 1995).

Finally, considering all aspects mentioned above, landscape ecology has become an umbrella discipline for many new fields of study that are dealing with the challenges of the Anthropocene. First, the concept of ecosystem services evolved from the early notion of multifunctional landscapes originally developed by landscape ecologists and planners. Ecosystem services are defined as the direct and indirect benefits that ecosystems—comprising species, communities, biotic and abiotic structures and processes—provide to human well-being (Daily et al. 2009, Seppelt et al. 2011). Ecosystem services were put in the spotlight by the Millennium Ecosystem Assessment (MEA), The Economics of Ecosystems and Biodiversity (TEEB), and the Intergovernmental Science-Policy Platform on Biodiversity and Ecosystem Services (IPBES) as a means to achieve the sustainable use of natural resources (Maes et al. 2012, Crossman et al. 2013). Since then, assessments of ecosystem services have become a common and effective policy tool for supporting decisions on land use because they can highlight benefits and trade-offs between different land-use options and because they integrate both biophysical and socioeconomic perspectives (Förster et al. 2015). Since the rapid changes of the Anthropocene era are eroding the resilience of biodiversity and ecosystems that underpin the provision of a large number of ecosystem services, investigating how landscapes simultaneously produce multiple ecosystem services is a crucial research frontier (Bennett et al. 2009, Mouchet et al. 2014).

Land system science is another sub-discipline embraced by landscape ecology. It centers around land systems which make up the terrestrial component of the Earth system and include all processes related to the human use of land. Land systems comprise also socioeconomic and organizational arrangements, as well as the benefits gained from land and the unintended social and ecological outcomes of societal activities (van Asselen and Verburg 2012, Verburg et al. 2013, 2015). Thus, land system science, organized around the Global Land Programme (GLP) community, serves as a platform to integrate different dimensions of global environmental change and study the mutual interplay between social and ecological systems that shape land use and land cover (Verburg et al. 2015). While initially land system science was dominated by remote sensing, monitoring and modelling the impact of land cover changes (e.g. deforestation or urbanization) on ecosystems, the current research field has become more integrative, focusing on both drivers and consequences of human–environment interactions. Current research topics span from teleconnections and modelling land system dynamics, through analyzing land use intensity, to trade-offs between different land-use forms and development trajectories (Verburg et al. 2011, 2013, van Vliet et al. 2016). Contributions to research areas in the scope of both the ecosystems services concept and land system science are covered by this habilitation thesis.

1.3 Scope of the thesis

In addition to introducing the Anthropocene and the discipline of Landscape Ecology, the presented habilitation thesis consists of three parts organized by the scale of studying the spatial aspects of human–environment interactions. The first part focuses on global issues, covering

topics of land system archetypes, global drivers and consequences of land-use intensity, and trade-offs between global agricultural production and biodiversity. The second part focuses on regional scales, covering topics of assessing ecosystem services and their bundles and the combined effects of climate and land-use change on ecosystem services. The third part focuses on local scales, drawing examples from research on local effects of land use and landscape heterogeneity on biological communities.

Most of the discussed findings are direct outcomes of research conducted within the scope of two international projects in which the author of this thesis served as a Principal Investigator: (1) the GLUES project (2009–2017) on Global assessment of land-use dynamics, greenhouse gas emissions and ecosystem services (<https://www.ufz.de/glues/>); and (2) the LEGATO project (2011–2017) on Land-use intensity and ecological engineering – assessment tools for risks and opportunities in irrigated rice based production systems (<http://www.legato-project.net/>).

The thesis is written in the form of briefly commented results of the author's research, which was typically published in the form of peer-reviewed papers in scientific journals with an impact factor under the Web of Science database. The author was closely and actively involved in producing these results and publications. Selected research papers are included in the appendix.

2 Global-scale dimensions of human–environment interactions

2.1 Global representation of land systems

Land use is the main representation of human–environment interactions and a key anthropogenic driver of global environmental change (Foley et al. 2005). Due to the rising demands for food, fiber and other commodities, the intensification of land-based production poses a major risk for the sustainable use of natural resources and ecosystem services (Seppelt et al. 2014). While land use is essential for human societies, it is also becoming increasingly clear that the current global land-use system is unsustainable. Transitioning to sustainable land-use systems that would balance growing resource demands with the conservation of ecosystems and biodiversity is therefore a central challenge for science and society (Foley et al. 2007, Rounsevell et al. 2012).

One approach to better understand the drivers and impacts of land-use intensification is the construction of land-use typologies based on identifying global, archetypical patterns of land systems. Traditional models of land systems are based largely on remotely sensed data of the terrestrial surface of the Earth (e.g. GlobCover, GLC 2000, CCI Landcover V2 remote sensing products). They typically focus on broad-scale representations of land cover with limited consideration of human influence or land-use intensity (Bartholome and Belward 2005, Arino et al. 2007). However, the recent surge in global-scale geospatial data pertaining to land management, such as cropland densities (Ramankutty et al. 2008), fertilizer use (Potter et al. 2010), or soil erosion (Van Oost et al. 2007), provide opportunities to incorporate indicators of land use and its intensity.

Several studies from the last decade made critical strides towards better integrating land-use and land management patterns in global representations of the earth's surface. For example, Ellis and Ramankutty (2008) suggested a new classification of anthropogenic biomes as an

innovative view of the human-dominated biosphere. These so-called anthromes were based on empirical analyses of global land cover, irrigation and population data, assuming that population density is a sufficient indicator of sustained human interactions with ecosystems. The anthrome concept was developed further by Letourneau et al. (2012) who proposed a classification of global land-use systems based on additional data on irrigation, livestock type and market accessibility. Similarly, van Asselen and Verburg (2012) improved the representation of land systems by including fractional land cover, livestock density and the efficiency of agricultural production for several staple agricultural crops, such as wheat, maize and rice.

All these studies had two aspects in common. First, they used mostly broad-scale representations of dominant land cover and biophysical factors with limited consideration of land-use intensity and other underlying conditions that constitute complex social-ecological systems (Ostrom 2009). Second, these studies applied top-down approaches to define land system classes based on a priori classification or on rules derived from expert's knowledge. To complement these efforts and reduce the level of subjectivity in the typology of land systems, an alternative approach is needed that would account for the various dimensions of land-use intensity and provide a typology of land systems driven mostly by empirical data rather than by predefined assumptions. Such approach is recommended to (i) better understand the interactions and feedbacks among different biophysical and social components of land systems, (ii) measure impacts that are currently difficult to quantify (e.g. effects of changing land-use intensity on biodiversity or social implications of land system transitions), and (iii) develop better policies and land management solutions adapted to regional conditions (Foley et al. 2011, Erb et al. 2013).

2.2 Land System Archetypes

Land System Archetypes (LSAs) provide a more holistic representation of global land system patterns, based on the integration of a wide range of global datasets on land-use intensity, environmental conditions and socio-economic indicators (Václavík et al. 2013). Here I provide an overview of the concept that our team developed within the GLUES project (Eppink et al. 2012) and give several examples that illustrate its use for (i) identifying drivers of ecosystem service risks, (ii) recognizing potentials to increase resilience of particular regions, and (iii) assessing transferability of findings from place-based research.

Land system archetypes are unique patterns of land use and its intensity within prevailing environmental and socio-economic conditions that occur repeatedly across the terrestrial surface of the earth (Václavík et al. 2013). We identified these archetypical patterns based on 32 land-use indicators available at the global scale (Table 1). These intensity indicators characterize land use in terms of inputs (e.g. extent of cropland, fertilizer input, irrigation), outputs (e.g. crop yields, production indicators) and properties of the social-ecological system (e.g. yield gap representing the difference between actual production and potential agro-ecological productivity) (Erb et al. 2013). Environmental indicators include climate, soil and vegetation characteristics that are known to drive and constrain the intensity and form of land use (Kuemmerle et al. 2013). Socio-economic indicators characterize the social, economic and political background of land systems (e.g. population density, gross domestic product, political stability, accessibility). Using self-organizing maps (SOMs), an unsupervised clustering technique that reduces high-dimensional

data by grouping observations based on their similarity and location, we characterized and mapped twelve land system archetypes at the global scale.

Table 1. Datasets used for classification of land system archetypes

Archetype factor	Spatial resolution	Unit	Source
<i>Land-use intensity factors</i>			
Cropland area	5 arc-minutes	km ² per grid cell	(Klein Goldewijk et al. 2011)
Cropland area trend	5 arc-minutes	km ² per grid cell	(Klein Goldewijk et al. 2011)
Pasture area	5 arc-minutes	km ² per grid cell	(Klein Goldewijk et al. 2011)
Pasture area trend	5 arc-minutes	km ² per grid cell	(Klein Goldewijk et al. 2011)
N fertilizer	0.5 arc-degrees	kg ha ⁻¹	(Potter et al. 2010)
Irrigation	5 arc-minutes	Ha per grid cell	(Siebert et al. 2007)
Soil erosion	5 arc-minutes	Mg ha ⁻¹ year ⁻¹	(Van Oost et al. 2007)
Yields (wheat, maize, rice)	5 arc-minutes	t ha ⁻¹ year ⁻¹	http://www.gaez.iiasa.ac.at/
Yield gaps (wheat, maize, rice)	5 arc-minutes	1000 t	http://www.gaez.iiasa.ac.at/
Total production index	national level	index	http://faostat.fao.org/
HANPP	5 arc-minutes	% of NPP ₀	(Haberl et al. 2007)
<i>Environmental factors</i>			
Temperature	5 arc-minutes	°C × 10	(Kriticos et al. 2012)
Diurnal temperature range	5 arc-minutes	°C × 10	(Kriticos et al. 2012)
Precipitation	5 arc-minutes	mm	(Kriticos et al. 2012)
Precipitation seasonality	5 arc-minutes	coeff. of variation	(Kriticos et al. 2012)
Solar radiation	5 arc-minutes	W m ⁻²	(Kriticos et al. 2012)
Climate anomalies	5 arc-degrees	°C × 10	http://www.ncdc.noaa.gov/cmb-faq/anomalies.php#grid
NDVI – mean	4.36 arc-minutes	index	(Tucker et al. 2005)
NDVI – seasonality	4.36 arc-minutes	index	(Tucker et al. 2005)
Soil organic carbon	5 arc-minutes	g C kg ⁻¹ of soil	ISRIC-WISE (ver 1.1)
Species richness	calculated from range polygons	# of species per grid cell	http://www.iucnredlist.org/technical-documents/spatial-data
<i>Socioeconomic factors</i>			
Gross Domestic Product	national level	\$ per capita	http://faostat.fao.org/
Gross Domestic Product in agriculture	national level	% of GDP	http://faostat.fao.org/
Capital Stock in agriculture	national level	\$	http://faostat.fao.org/
Population density	2.5 arc-minutes	persons km ⁻²	CIESIN database
Population density trend	2.5 arc-minutes	persons km ⁻²	CIESIN database
Political stability	national level	index	http://www.govindicators.org
Accessibility	0.5 arc-minutes	minutes of travel time	http://bioval.jrc.ec.europa.eu/products/gam/index.htm

The map of global archetypes reveals a clustered pattern of land systems across the world, ranging from barren and marginal lands with low land-use intensities, through pastoral and forest mosaic systems, to intensive cropping systems dominated by high agricultural inputs (Figure 2). The combination of land use indicators and the underlying conditions that best characterize each

archetype is summarized in Figure 3. The results show unexpected similarities in land systems in many regions (e.g. the extensive cropping systems archetype in East Europe, India, Argentina and China) but also a diversity of land-use forms at a sub-national scale, such as in China or India. These archetypal patterns imply that place-based approaches are needed to develop regional strategies for sustainable management of land and ecosystem services (Václavík et al. 2013, 2019).

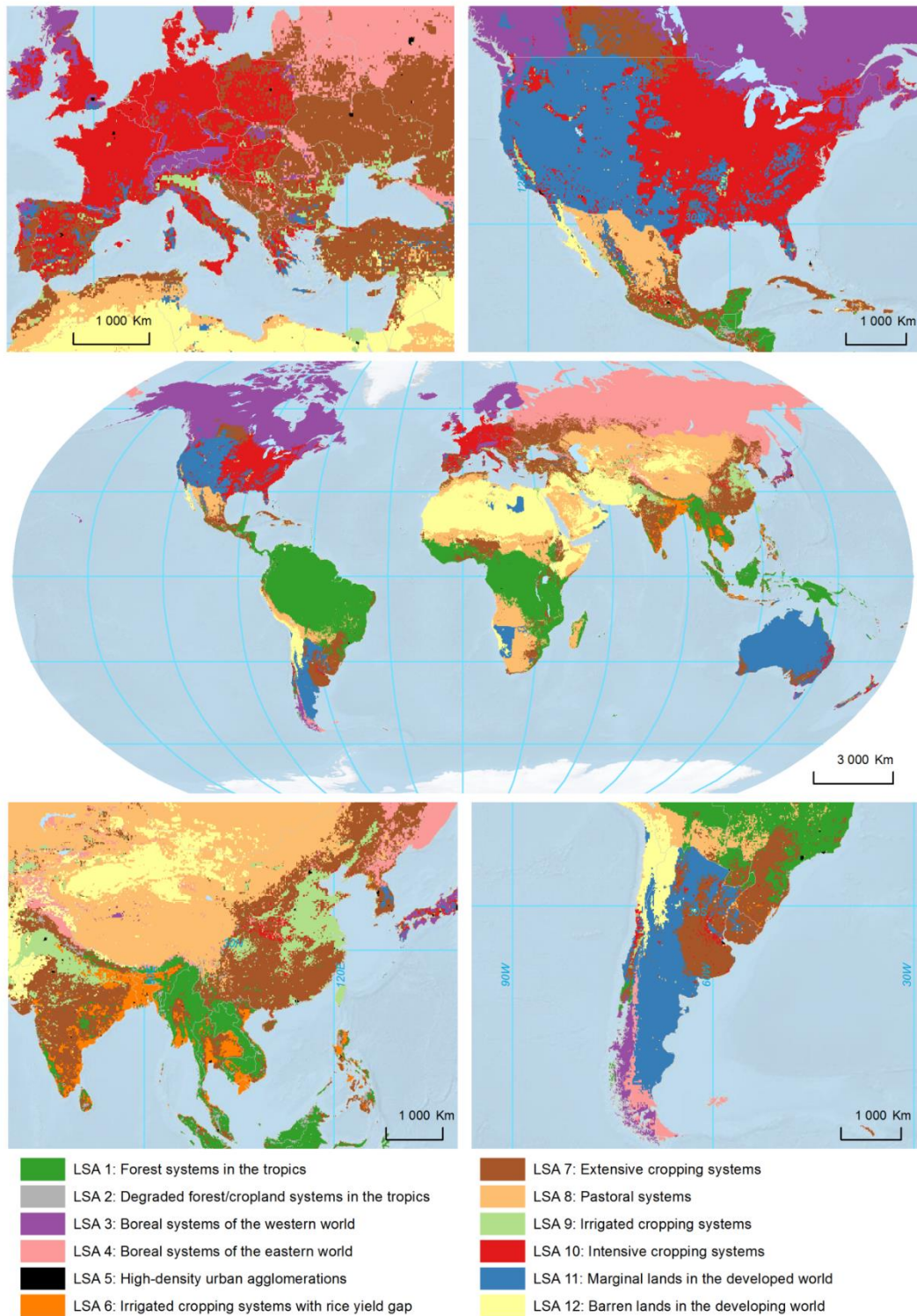


Figure 2. Global land system archetypes; world map and regional areas. Adopted from Václavík et al. (2013).

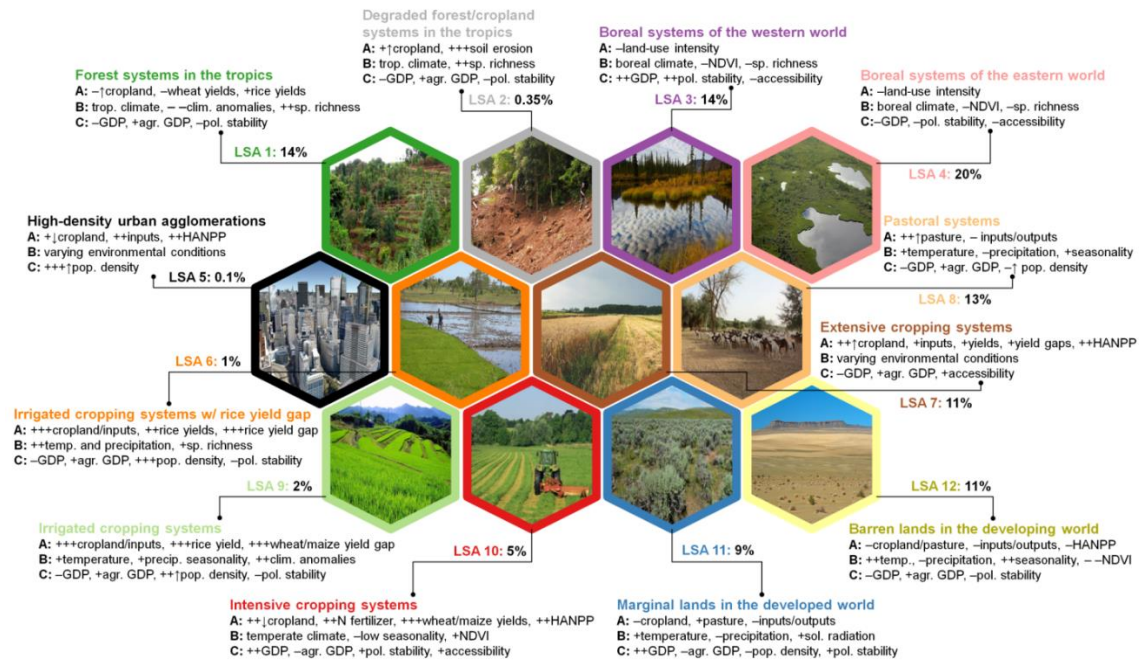


Figure 3. Overview of land system archetypes, summarizing major land-use intensity indicators (A), environmental conditions (B) and socio-economic factors (C) that best characterize each archetype (for list of variables see table 1). The + and – signs show whether the factor is above or below global average (+ is up to 1 s.d., ++ is 1–2 s.d., +++ is > 2 s.d.); the ↑ and ↓ signs signify increasing/decreasing trends within the last 50 years; the numbers represent percentages of terrestrial land coverage. Adopted from Václavík et al. (2013).

The archetype approach facilitates an integrative understanding of land systems and provides insights into potential drivers of and impacts on ecosystem services, which may remain uncovered if they are studied in isolation. For example, archetypes help identify generic patterns of land pressures and ecosystem service risks, such as the risks to food provisioning due to soil erosion. Based on the considered land-use indicators, several regions in the tropical Latin America and Southeast Asia are classified as "degraded forest / cropland systems in the tropics" (Figure 2 and 3). These systems are characterized by extremely high soil erosion (>3 s.d. above global mean) and represent areas where patches of rainforest were converted to cropland. Although soil erosion occurs in other systems too, these regions are particularly affected by the loss of soil fertility because of their high agricultural inputs, relatively poor economy and strong dependence on agricultural production (Figure 3). The underlying socio-economic data, showing that food production is important for the national economy of the local countries, emphasize the need to develop and apply erosion control measures for these regions. Therefore, this archetype pinpoints regions that may require similar policy responses and highlights regional heterogeneity (e.g. within countries) which decision makers should consider. Although data on forest management intensity are not available globally, this archetype matches well with the hotspots of forest cover change (Hansen et al. 2013).

The land system archetype approach also allows providing science-based recommendations for regions with certain land-use types on how to identify opportunities to increase resilience of agricultural systems (Václavík et al. 2019). It has been recognized that new approaches to agriculture that would prevent cropland expansion, close yield gaps and increase cropping efficiency should be implemented to sustain future food demands while shrinking

agriculture’s environmental footprint (Foley et al. 2007). Analyses of land systems can help identify farming strategies and support the development of solution portfolios relevant for a particular place. For instance, while the differences between realized and attainable yields are relatively small in “intensive cropping systems”, considerable opportunities for yield improvements exist in the “extensive cropping systems” archetype (Figure 4). This is in congruence with other studies (Mueller et al. 2012, Zabel et al. 2014) showing that Eastern Europe and Sub-Saharan Africa represent relatively easily achievable opportunities for intensification of wheat and maize production through nutrient and water management. Such regions have high potential for enhancing their food security by increasing their cropland production to only 50% of attainable yields. Considering that many of these regions are characterized by a considerably low political and economic stability, any type of land management, no matter if focusing on adaptation to climate change or closing yield gaps, needs to consider the limitations of land-use options due to social and political constraints (Václavík et al. 2013, 2019).

Finally, the concept is also useful from an applied, methodological point of view. Its modification has been successfully used as a method for investigating the transferability of findings from place-based research, e.g. case studies focusing on different aspects of sustainable land management across four continents (Václavík et al. 2016). Case studies, rooted in a particular place and context, are the main means of deriving knowledge on land systems and the goods and services they provide (van Vliet et al. 2016). However, the generalization and transferability of results from place-based case studies is inherently limited because the drivers and processes of land use are complex, and their outcomes are contingent upon specific geographical context, including prevailing environmental, socioeconomic and cultural conditions. Drawing generalized conclusions about practical solutions to land management from local observations and formulating hypotheses applicable to other places in the world requires that we identify patterns of land systems that are similar to those represented by the case study.

Therefore, Václavík et al. (2016) estimated the transferability potentials for twelve regional case studies of the GLUES project (Eppink et al. 2012) by calculating the statistical similarity of all locations across the world to the unique land system archetype present in each study area (Figure 4). This case study archetype was defined by the multi-dimensional space of considered land-use intensity, environmental and socioeconomic variables, assuming higher transferability potentials in locations with similar land systems. An absolute distance D was used as a measure of similarity, calculated as:

$$D = \frac{1}{g \times p \times v} \sum_{i=1}^v \sum_{n=1}^p \sum_{m=1}^g |x_{i,n} - x_{i,m}|$$

with x being the normalized value of variable i , g being the number of global grid cells, p being the number of cells within a regional case study and v being the number of considered variables. Using the inverse of distance D , the gradient of transferability potentials for each project was mapped in the geographical space (Figure 4). In this study, results showed that areas with high transferability potentials were typically clustered around case study sites but for some case studies were found in regions that were geographically distant, especially when values of considered variables were close to the global mean or where the case study archetype was driven

by large-scale environmental or socioeconomic conditions. This method allows taking information from a specific case study and identifying other unstudied areas that may face similar land-use challenges and therefore benefit from transferring the existing knowledge and solutions to land management problems. The method also provides a blueprint for large research programs to assess potential transferability of place-based studies to other geographical areas. Several European research projects have already applied this methodology, e.g. the TALE project (<https://www.ufz.de/tale/>).

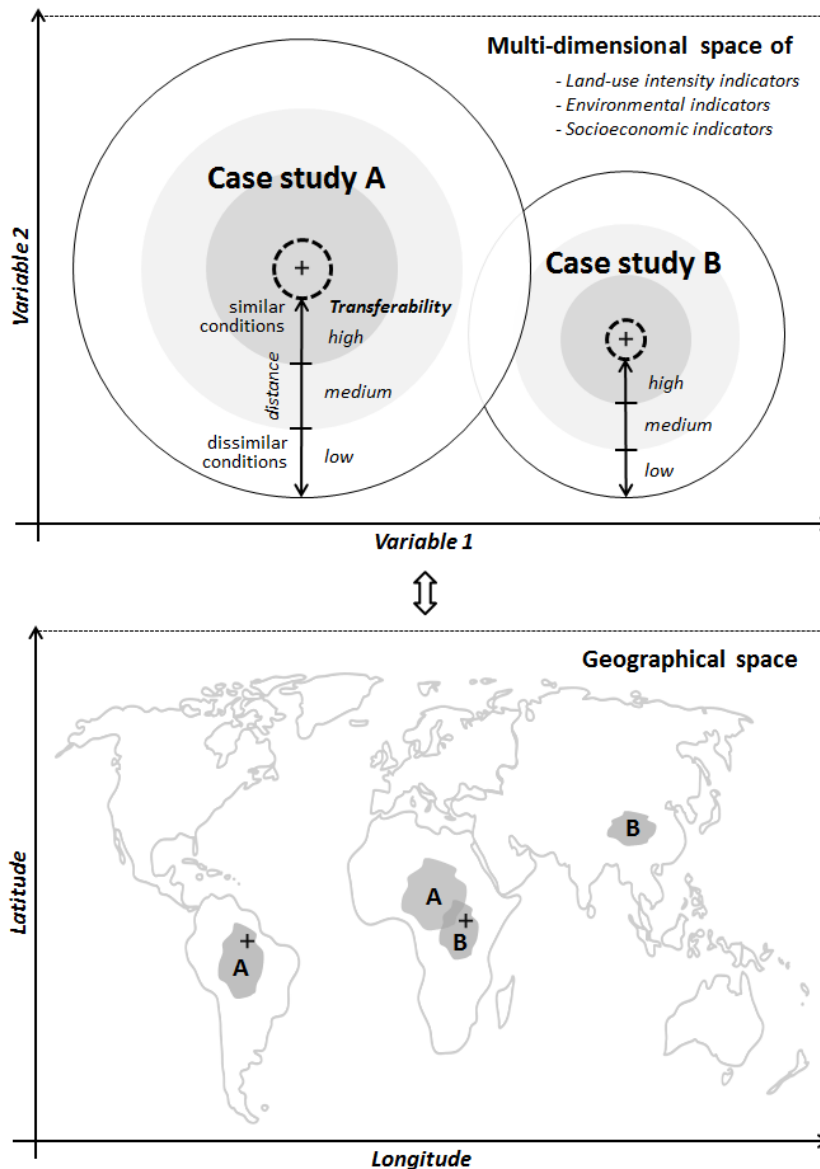


Figure 4. Conceptual diagram of mapping potential transferability of place-based research. The upper rectangle represents a multidimensional space defined by land-use intensity, environmental and socioeconomic indicators. The crosses denote the ‘case study archetypes’, i.e. the mean conditions in the areas of two hypothetical case studies; the circles denote the range of conditions; different shading representing similarity of conditions. The distance does not represent a geographical distance but a statistical measure of similarity of the considered variables. This distance can be mapped in a geographical space (lower rectangle), here showing the ‘high’ level of similarity (i.e. transferability potential) for each case study, with crosses denoting the location of the hypothetical study areas. Land systems similar to case study archetypes may differ in size or overlap in the multi-dimensional or geographical space. Adopted from Václavík et al. (2016).

2.3 Spatial patterns of land use and global biodiversity

Land use, and its various forms, intensities and change in different types of land systems, is also one of the biggest drivers of the ongoing biodiversity crisis. Land-based production faces increased demands due to growing human population, surging consumption and changing diets. Thus, it can be reasonably expected that the pressure from agricultural production on biodiversity will escalate further (Tilman et al. 2011). As biodiversity loss can have serious repercussions on ecosystems functioning and the resilience of social-ecological systems, understanding where and how agricultural land use puts pressure on biodiversity is of prime importance (Kehoe et al. 2015, Fischer et al. 2017).

Agricultural land use threatens biodiversity mainly through the loss, degradation and fragmentation of natural habitats (Pereira et al. 2012, Newbold et al. 2015). Thus, studying the effects of cropland expansion and land transformation on biodiversity has received much attention in the scientific literature (Pereira et al. 2010, Hosonuma et al. 2012, Chaplin-Kramer et al. 2015). On the other hand, effects of land-use intensification remains poorly understood, despite the evidence that land-use intensification threatens multiple taxa of primarily farmland species due to habitat homogenization, irrigation and high inputs of agro-chemicals, such as fertilizers and pesticides (Kleijn et al. 2008, Seppelt et al. 2016). This is particularly worrying because intensification processes and their impacts vary across the globe and because agricultural intensification is increasing rapidly due to the scarcity of fertile land and the environmental costs associated with the conversion of natural habitats (Rudel et al. 2009).

The main reason for this knowledge gap is that (i) land-use intensity is intrinsically complex and multi-dimensional issue and (ii) consistent datasets for the different dimensions of land-use intensity have been lacking until recently, especially at the global scale. Land-use intensity metrics can either address inputs (e.g., fertilizer, irrigation), outputs (e.g., yields, production indices), or the land system as a whole (e.g., yield gap, the amount of biomass removed) (Erb et al. 2013, Kuemmerle et al. 2013). Several recent studies, however, embraced the new developments in land-use intensity framing, high-resolution global datasets and global biodiversity indicators and analyzed how spatial patterns of land use coincide with biodiversity patterns.

In Kehoe et al. (2015), we compiled a geodatabase of thirteen complementary global land-use intensity metrics consistently available for the situation around the year 2000. These metrics were then compared with a global biodiversity indicator, namely endemism richness for birds, mammals and amphibians, which is a metric that combines species richness with the area of each species geographical range, indicating a relative importance of given area for global conservation (Kier et al. 2009). Through concordance maps and spatial statistics, including the local indicator of spatial association (LISA), we identified statistically significant spatial associations between current land-use intensity and biodiversity.

Two main insights can be drawn from this analysis. First, areas where high-intensity agriculture puts pressure on regions with the highest biodiversity value are found primarily in the tropics. However, more than 40% of such potential conflict areas for all three taxa are outside the biodiversity hotspots designated by Conservation International. Such areas include Papua New Guinea, Venezuela, parts of China, Eastern Africa and Eastern Australia (Figure 5). Because to date, no established conservation prioritization scheme has considered land-use intensity metrics,

highlighting areas under high pressure from agricultural intensity may merit increased conservation attention. Second, consideration of different land-use intensity metrics results in diverse spatial patterns associated with biodiversity. For example, for input metrics, high conflict potential occurs in China, Southeast Asia and parts of Europe for high fertilizer use, in the USA, India and Middle East for high irrigation, and in Latin America and India for high livestock densities. For output metrics, oil palm plantations show high concordance with biodiversity especially in Nigeria, Malaysia and Indonesia, while soy bean cultivation is particularly high in ecologically valuable regions of Brazil, Argentina and Indonesia (Figure 5). The broad range of spatial patterns identified for different types of land-use intensity metrics suggests that traditional risk assessments focusing on single indicators of land use may severely underestimate biodiversity risk. Therefore, a wider spectrum of land-use intensity indicators is needed when developing strategies to balance agricultural activities with biodiversity conservation.

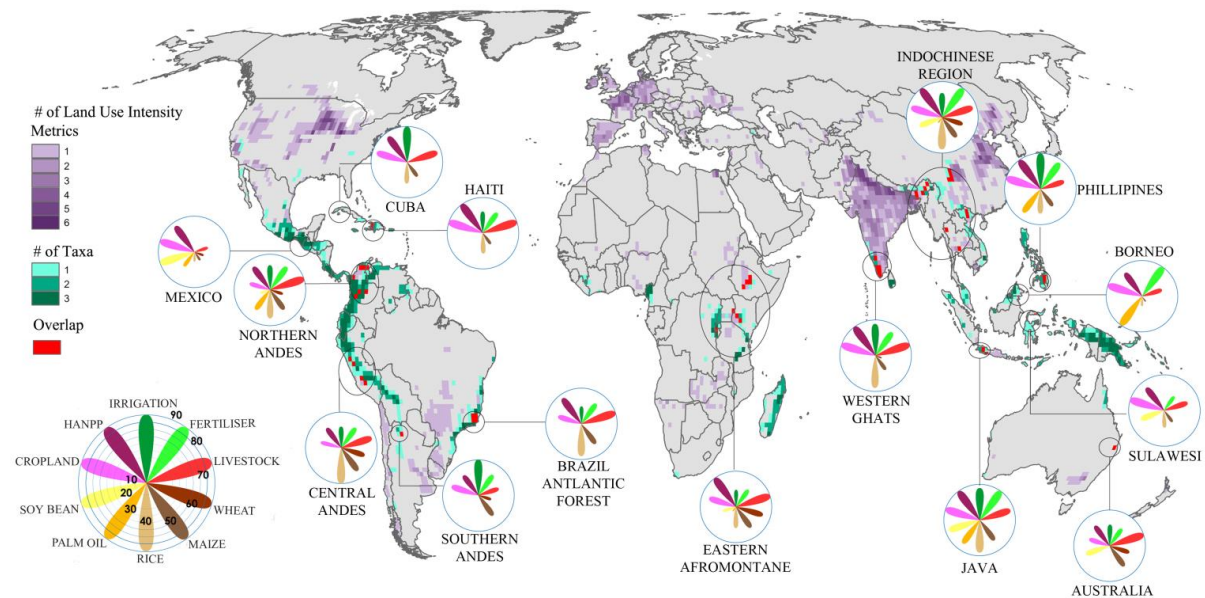


Figure 5. Top 2.5% of current land-use intensity (LUI) and biodiversity, where any of the top 2.5% intensity metric overlaps with any of the top 2.5% of endemism richness for mammals, birds and amphibians, thus highlighting regions of particularly high pressure between human activity and wildlife. Multiple overlapping LUI metrics of top 2.5% are shown in purple and multiple high endemism richness for taxa shown in green; overlap between LUI and endemism richness in red. 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. Adopted from Kehoe et al. (2015).

Recent research has investigated not only the current but also the expected future patterns of land-use impacts on biodiversity and crop production (Mauser et al. 2015, Kehoe et al. 2017, Egli et al. 2018). One of the major research goals in this area is to identify and assess the trade-offs between biodiversity and different future scenarios of global agricultural pathways. Typically, agricultural land-use change occurs in two main forms: expansion of cropland into uncultivated areas, or intensification of already existing agricultural lands (Kehoe et al. 2015). While both pathways are likely to occur simultaneously in order to meet the future demand for food and other agricultural commodities, we have only a limited knowledge of where one pathway

is more likely over the other and how their impacts on biodiversity will manifest in different regions.

Within the GLUES project (Eppink et al. 2012), we attempted to (i) quantify the relative differences in the impact of alternative global farming strategies (cropland expansion vs. intensification) on crop yields and crop prices, and to (ii) identify hotspots of potential future conflicts between cropland expansion, intensification and biodiversity (Delzeit et al. 2017, Zabel et al. 2019). We combined two established approaches from previous research (Zabel et al. 2014, Mauser et al. 2015), which integrate both biophysical and socio-economic conditions to create maps of future cropland expansion and intensification potentials simulated for 17 major agricultural crops at 30 arc-sec spatial resolution. These integrated potentials of cropland expansion and intensification account for the interplay of biophysical constraints at the local scale, such as water availability, soil quality and climate change, and regional socio-economic drivers, such as population growth and dynamics in consumption patterns. Then, we examined the impact of cropland expansion and intensification on agricultural markets. To do so, we applied a computable general equilibrium (CGE) model of the world economy that accounts for interlinkages between economic sectors to two comparable scenarios of cropland expansion and intensification until 2030. The cropland expansion scenario allowed additional land to be available for crop production in areas with the highest 10% of global expansion potential. Comparably, the cropland intensification scenario allowed closing yield gaps on 10% of land with the highest global intensification potential, up to the level that both scenarios led to equivalent global production gains. Finally, we used global range maps for almost 20,000 vertebrate species to examine the spatial concordance between patterns of global biodiversity and potentials for near-future cropland expansion and intensification.

Both farming scenarios by 2030 are likely to improve food security not only in regions where crop production rises but also in regions that may experience decline in crop production and will have to import crops. This is caused by the expected surplus of crops and therefore lower crop prices at the world market. For example, both the expansion and intensification scenarios show an increase in crop production, e.g., in Sub-Saharan Africa and Australia, but contradicting impacts in other world regions; e.g. crop production increases significantly in Central and South American countries under the cropland expansion scenario, while it decreases under the intensification scenario. On the other hand, the estimated cropland expansion and intensification is likely to take place in many highly biodiverse regions (Figure 6).

These regions are located overwhelmingly in the tropics, with cropland expansion affecting larger areas than cropland intensification (significant hotspots covering 14% and 8% of the terrestrial ecosystems, respectively). Cropland expansion threatens biodiversity hotspots especially in Central and South America, including the western part of the Amazon Basin and the Atlantic forest, in the forests and savannahs of Central Africa and Madagascar, as well as in parts of South Africa, Eastern Australia and large portions of South-East Asia (Figure 6A). The cropland intensification pressure on biodiversity is generally less pronounced, especially in Latin America, but includes regions in Sub-Saharan Africa, India, Nepal, Myanmar and China where farming intensity is projected to increase substantially in 2030 (Figure 6B). The hotspots of future potential conflict for birds and mammals show high spatial agreement (64% and 66% overlap for cropland expansion and intensification, respectively). However, areas of high agricultural potentials associated with high endemism richness are relatively smaller for amphibians (41% and 40%

overlap with the other taxa) due to the smaller ranges of amphibian species concentrated in specific geographical areas (Zabel et al. 2019).

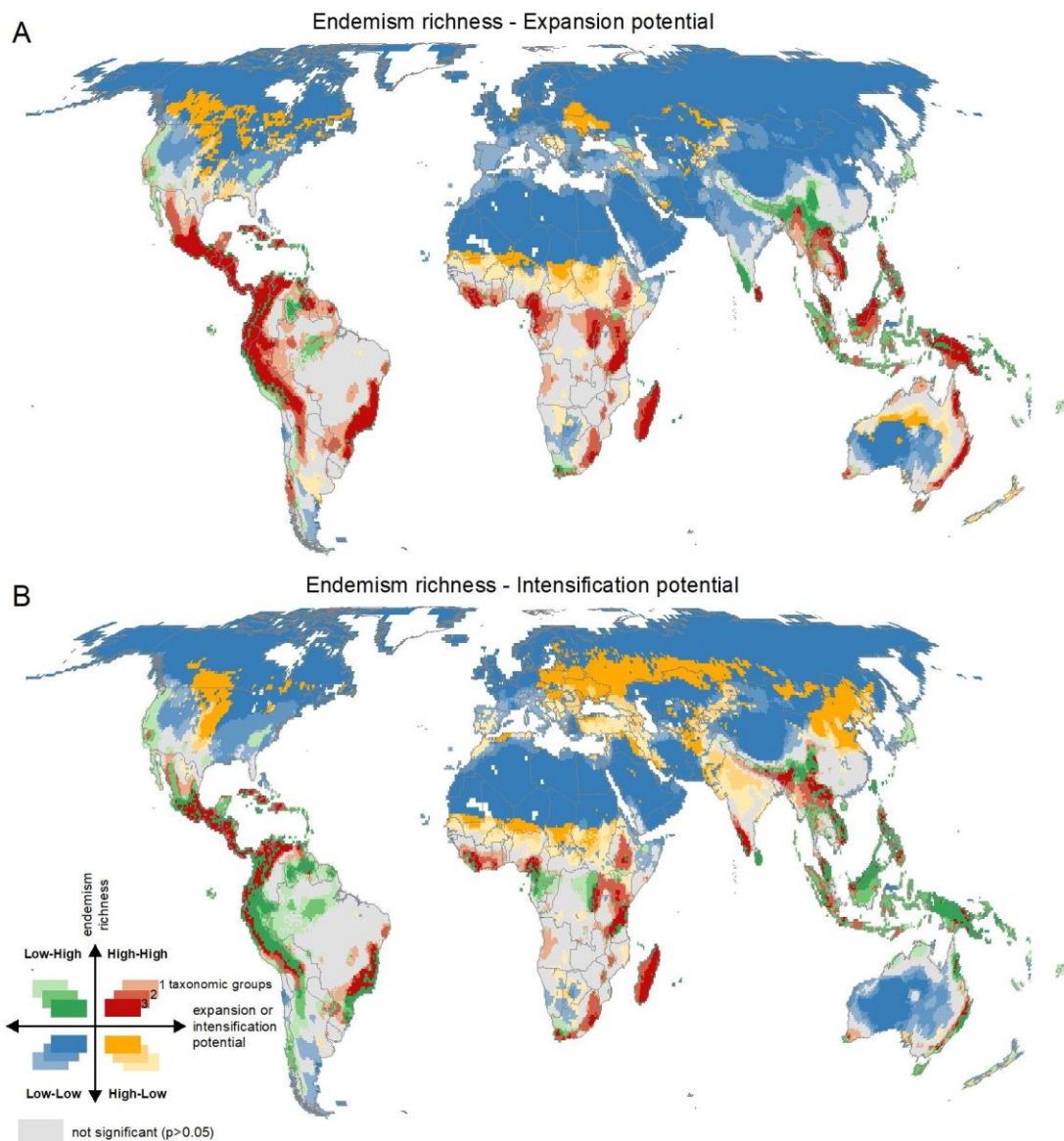


Figure 6. Spatial association between endemism richness and potentials for future (A) cropland expansion and (B) intensification calculated using local indicators of spatial association (LISA) at 55-km resolution. High–high clusters indicate hotspot locations (red), in which areas most suitable for expansion/intensification of cropland are significantly associated with high values of endemism richness (at 0.05 significance level). Low–low clusters (blue) show cold spot locations, in which areas with low potential for expansion/intensification are associated with low values of endemism richness. High–low and low–high clusters show inverse spatial association. Three shades of colors indicate significant results for one, two or all three taxonomic groups (birds, mammals, amphibians). Adopted from Zabel et al. (2019).

On the other hand, these analyses also allow identifying areas where high potential for future expansion or intensification of agriculture pose lower threats to conservation of global

biodiversity (Figure 6, high–low orange cluster). For example, regions with the highest production gains under the intensification scenario occur in Eastern Europe, Sub-Saharan Africa, Central India, Northeast China or Former Soviet Union. These regions coincide with the ‘extensive cropping land system archetype’ (Václavík et al. 2013) where large production gains could be achieved by closing yield gaps through nutrient and water management (Mueller et al. 2012) without necessarily promoting additional decline in biodiversity on the current farmlands, e.g. via the use of precision or climate-smart agriculture. However, even regions with relatively low endemism richness at the global scale are often considered strongholds of farmland biodiversity regionally, or include cultural heritage that cropland expansion or intensification may threaten (Delzeit et al. 2017). Therefore, more context-specific assessments that consider a range of ecosystem services, cultural and political background, and the resilience of land systems are needed to better understand the outcomes of different agricultural pathways (Rudel et al. 2009, Delzeit et al. 2017, Kehoe et al. 2017)

3 Regional-scale dimensions of human–environment interactions

3.1 Ecosystem service synergies and trade-offs

The regional assessment of relationships among ecosystem services (ES), i.e. the benefits that human societies obtain from ecosystem functioning and biodiversity, is another approach in landscape ecology to examine the spatial aspects of human–environment interactions. Several recent studies have helped conceptualize and recognize the importance of ES relationships (Bennett et al. 2009, Raudsepp-Hearne et al. 2010, Mouchet et al. 2014, Cord et al. 2017, Spake et al. 2017). ES can be associated either in a complementary way (synergy) or a conflicting way (trade-off) such that changes in one ES cause or lead to changes in another or multiple ecosystem services (Bennett et al. 2009). However, the terminology is not always consistent in ES literature. For example, synergy has been sometimes defined as the positive response of multiple ES to a change in the driver (Bennett et al. 2009), while other times as a win-win situation that involves a mutual improvement of two or more ecosystem services (Haase et al. 2012). On the other, trade-offs are understood more consistently in the literature, describing an antagonistic relationship when a quality or value of one ES is lost in return for gaining another ES and therefore requires choices to be made between alternatives that cannot be achieved at the same time (Crouzat et al. 2015, Cord et al. 2017).

In Cord et al. (2017), we reviewed the large body of literature on ES and identified two main objectives for analyzing ES relationships (Figure 7). The first objective is to identify, characterize and map co-occurrences of ES (so-called ES bundles), in particular those, which are positively or negatively associated (Figure 7a). This approach provides insights into (i) what ES are provided and can be used simultaneously in the same region and (ii) whether the presence of one service limits the presence of another service (Crouzat et al. 2015). However, this approach usually does not involve examining the causal relationships among considered ES. Therefore, typical methods applied for this objective include pairwise correlations tests or clustering methods, such as K-means clustering or Principal Component Analysis (PCA), the latter used to identify typical bundles of ES. Sometimes, simple descriptive methods, e.g. in the form of spider or flower diagrams are used (Cord et al. 2017).

The second main objective is to identify drivers, environmental or social pressures, and underlying mechanisms of ES relationships (Figure 7b). These studies go beyond describing ES co-occurrences and focus on how drivers of ES may have positive or negative effects on multiple ES simultaneously. For example, Bennett et al. (2009) illustrates this situation on, e.g. fertilization, which on one hand may increase agricultural yield (provisioning ES) but at the same time negatively affect pollination or local provisioning of clean water (regulating ES). Another possibility is that relationships among ES are caused by direct relationships among the services. For instance, ES may interact positively, e.g. when retaining forest patches near coffee plantations increases pollination, which in turn increases coffee production (Bennett et al. 2009). However, the scale of the analysis and ES mapping is highly important for determining causal relationships among multiple ES. In some cases, no effect is found only due to the scale mismatch of analyzed ES, e.g. several ES may co-occur in the same spatial unit (watershed or district), although at finer spatial scale they do not spatially overlap (Mouchet et al. 2014).

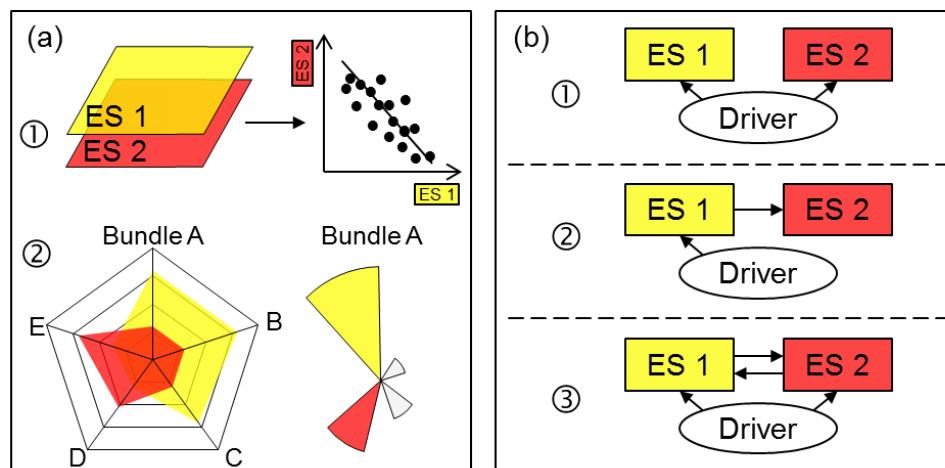


Figure 7. Main goals of studies on ES relationships. (a) Identifying and describing ES co-occurrences: ① Spatial overlay of ES maps and correlation analysis, ② Illustration of ES bundles using spider diagrams (showing multiple bundles A-E) or flower plots (for bundle A); (b) Identifying drivers, environmental or social pressures and underlying mechanisms: ① Common environmental or socio-economic drivers lead to or reinforce the observed trade-offs or synergies, ② Direct interactions between ES lead to trade-offs or synergies, ③ Combined effects of ① and ②. Adopted from Cord et al. (2017).

3.2 Regional mapping of ecosystem service bundles

A recent example that illustrates the objective of mapping ES co-occurrences is the study by Dittrich et al. (2017). Here, we analyzed the relationship and spatial distribution of multiple ES in the context of underlying socio-environmental conditions as a part of the national ecosystem assessments in Germany. We proposed a reproducible approach, which identifies ES bundles and serves as a blueprint to assist other EU member states in fulfilling the basic requirements of the EU Biodiversity strategy to 2020. This is because the EU Biodiversity strategy declares the aim of “maintaining and restoring ecosystems to ensure the continuous provision of ecosystem services”. This aim is specified in Action 5 of Target 2, which requires EU member states to “map and assess the state and economic value of ecosystems and their services” and to “promote the recognition

of their economic worth into accounting and reporting systems across Europe". Mapping the spatial patterns of ES bundles is an effective way of synthesizing information on ES for decision makers to be used in national or sub-national ES assessments (Schröter et al. 2016).

The proposed approach consists of three methodological steps (Dittrich et al. 2017). The first step includes collection and harmonization of spatial data on ecosystem service indicators. Some of the main criteria for selecting ES indicators involve data availability, geographical coverage and representativeness of different ES categories. Ideally, the ES indicators are available on a regular basis (e.g. quarterly, yearly), so the analysis can be repeated and trends in ES change monitored. All used indicators should cover the entire study region or nation and be available at a sufficient grain (minimal unit of analysis), e.g. the regular grid of 10 x 10 km (Figure 8) based on the standardized European equal-area reference system developed for statistical mapping (ERTS89). The ES indicators should cover provisioning, regulating as well as cultural services and their selection can be guided by the indicator framework developed for assessing ES in support of the EU Biodiversity Strategy to 2020 (Maes et al. 2016). The second step is centered around the employment of self-organizing maps (SOM), an unsupervised clustering technique based on artificial neural networks, which reduce high-dimensional data by clustering observations based on their similarities and thus it is highly suitable for spatially-explicit mapping of ES bundles (Agarwal and Skupin 2008, Mouchet et al. 2014). Finally, the spatial pattern of identified ES bundles is compared against a set of environmental and socioeconomic covariates.

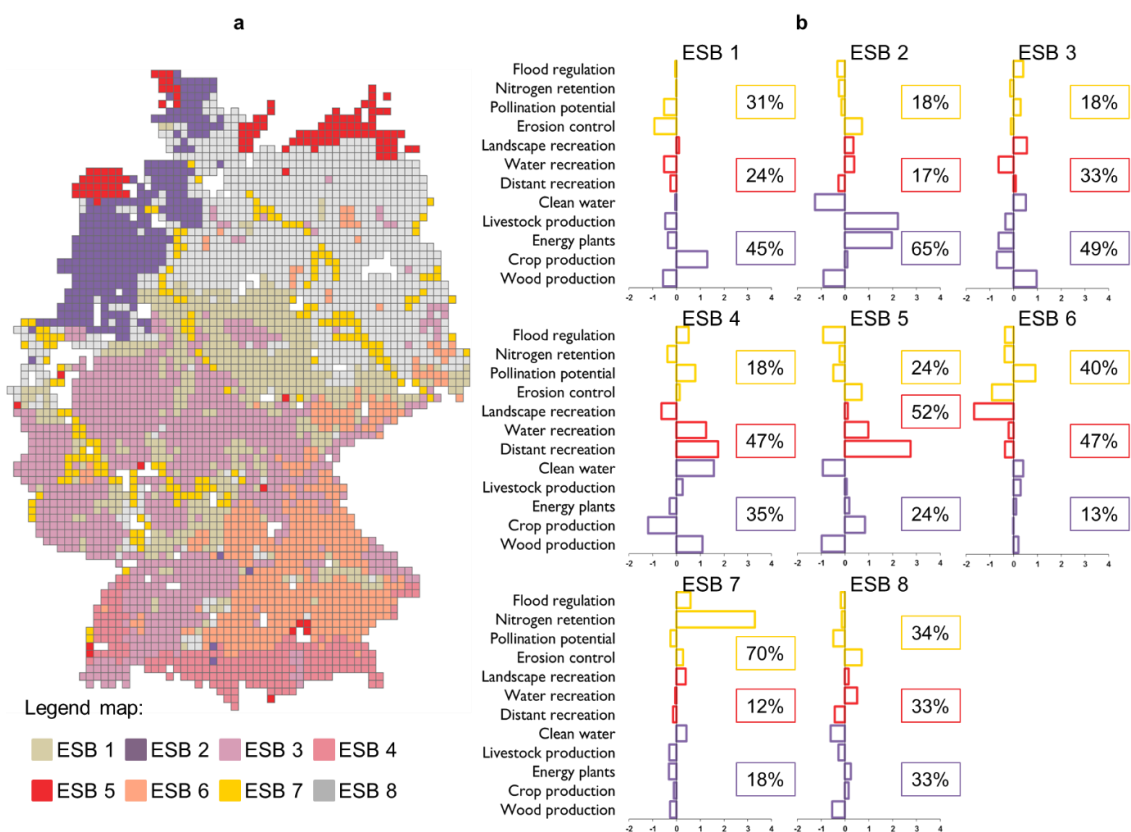


Figure 8. Ecosystem service bundles mapped in Germany (a). The bar plots (b) show the z-score normalized values of ES indicators that best characterize each bundle, with zero representing the national average. The relative contribution of the three ES categories to each bundle is indicated by the percentages next to the bar plots (purple: provisioning, red: cultural, yellow: regulating/maintenance). Percentage ratios per ES bundle are based on the total absolute values of the ES indicators. Adopted from Dittrich et al. (2017).

Several insights about the regional-scale patterns of human–environment interactions can be drawn from such analysis. First, the analysis for Germany identified and mapped eight ES bundles characterized to varying degrees by provisioning, cultural and regulating/maintenance services (Figure 8). It shows that bundles dominated by cultural ES are associated with areas where environmental and socio-economic gradients had similar importance, but those ES bundles that were dominated by provisioning ES occurred in regions with distinct environmental characteristics. This reflects the ongoing specialization in land use and specifically in agricultural management practices (Raudsepp-Hearne et al. 2010, Dittrich et al. 2017). On the other hand, some regions, e.g. in north-eastern Germany, have no clear specialization in provisioning, regulating or cultural services, indicating a more multifunctional use of landscapes. Second, synergies and trade-offs among ES can be detected across the study area. Exemplary results from these analyses are trade-offs between livestock farming and provisioning of clean water or between crop production and landscape-related recreation. These findings highlight future research avenues that should focus on the causal mechanisms behind ES associations that are important for landscape management and planning.

3.3 Combined effects of land-use and climate change on ecosystem services

Understanding the drivers and underlying mechanisms of ES relationships requires the use of sophisticated methods that combine empirical data, spatially explicit modeling and sometimes the employment of scenarios that help assess the potential future trends in ES values and the relationships among them. In the LEGATO project, which focused on ecological engineering and ES in irrigated rice agro-ecosystems in the Philippines and Vietnam (Settele et al. 2018, Spangenberg et al. 2018), we have applied such approach to examine the combined effect of climate and land-use as underlying drivers of ES change in the future (Langerwisch et al. 2018).

Irrigated rice agro-ecosystems are some of the most important ecosystems globally. Besides providing food for ca 3.5 billion people, they provide a range of other ES. These include the provision of fuel and fiber, regulation of water supply for irrigation and fishing, nutrient cycling and carbon sequestration, but also cultural services such as cultural identity associated with traditional rice farming (Burkhard et al. 2015). However, the sustainability of rice agro-ecosystems is threatened by continuing climate and land-use changes. To estimate their combined effects on a bundle of ES in seven study areas in the Philippines and Vietnam (Figure 9), we analyzed satellite land cover data, developed future climate and land-use scenarios and applied a vegetation and hydrology model to simulate future trends in ES (Langerwisch et al. 2018).

The provision of ES can be estimated not only through directly measured ES indicators but also, e.g., by the hydrology and vegetation model LPJmL (Metzger et al. 2008). In Langerwisch et al. (2018), LPJmL was used to simulate future changes in the provision of four essential ES: carbon storage, carbon sequestration, provision of irrigation water and rice production. These future changes were quantified under two climate scenarios until 2100 (SRES scenarios B1 and A2) and three site-specific land-use scenarios until 2030. The climate change scenarios were developed at a 30 m resolution by downscaling data from the General Circulation Model MPI-ECHAM5, using lapse rate adjustment to correct for the effect of topography. Land-use scenarios were developed based on land cover data from SPOT5 satellite images and expert's estimations of future

developments for the dominant land cover categories, resulting in one conservative and one extreme scenario.

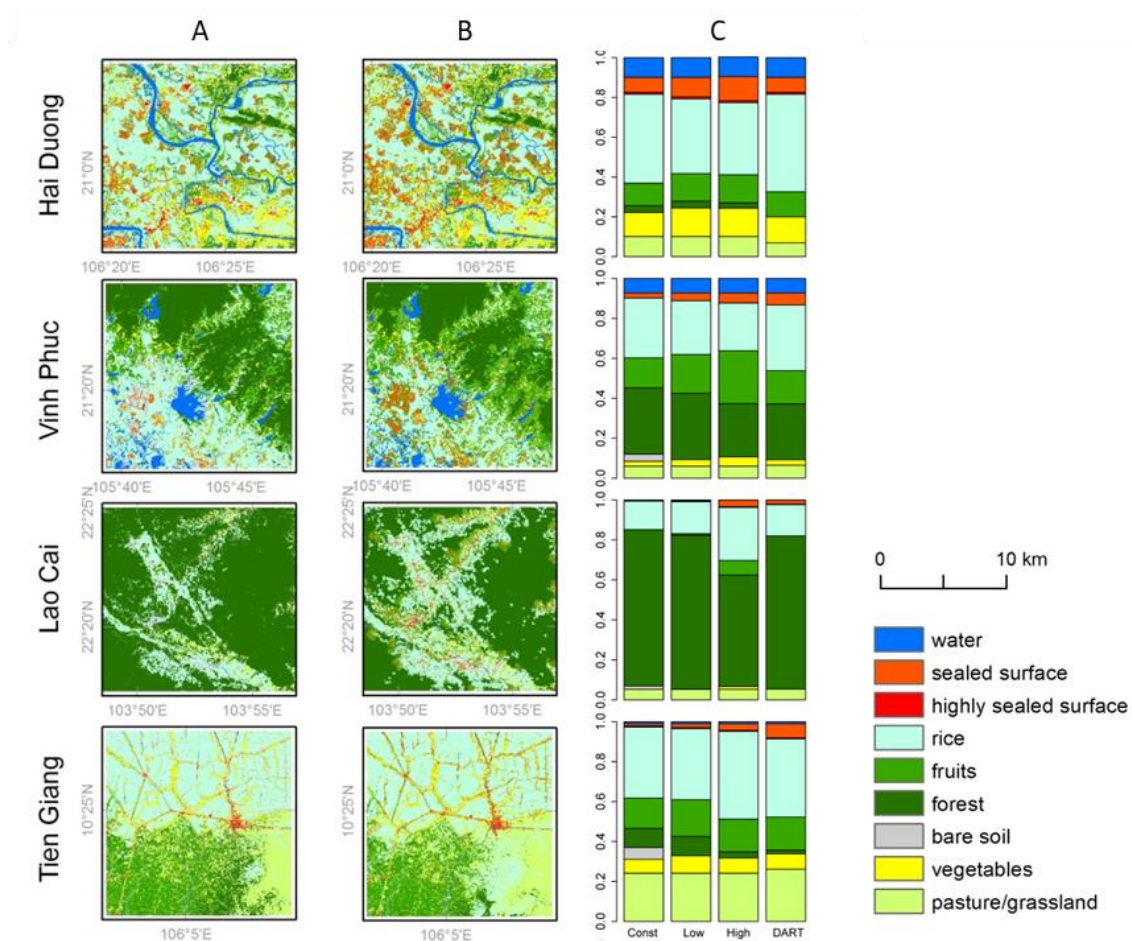


Figure 9. Land use classes in four study areas in Vietnam. (A) Observed land use class, (B) land use in 2030 in the High-conversion scenario and (C) fraction of land use categories in 2030 in all land use change scenarios (Low-conversion, High-conversion and DART). The land use scenario ‘Const’ refers to the observed land use. Adapted from Langerwisch et al. (2018).

For rice agro-ecosystems in the Philippines and Vietnam, climate and land-use change in combination is likely to reduce the provision of most ES (Figure 10). With the exception of irrigation water, whose provision increases due to higher expected precipitation levels, climate change alone causes a considerable decrease in ES by the end of the 21st century. The effect of land use change is comparatively smaller. However, where unmanaged land is available, new land conversion may allow partially offsetting negative impacts of climate change, although only at the expense of natural habitat. Loss of natural habitat is typically accompanied by biodiversity degradation and a range of cultural and societal implications (Spangenberg et al. 2018), which make managing rice agro-ecosystems for multiple ES challenging. This is complicated also by the fact that multiple ES are often provided by the same type of land use but they do not always respond the same way to climate and land-use change drivers (Burkhard et al. 2015, Spake et al. 2017). In Asian rice croplands, such trade-offs can be found, e.g., between irrigation water versus carbon storage, carbon sequestration and rice production (Burkhard et al. 2015, Langerwisch et

al. 2018). The provision of irrigation water shows consistently positive response under combined climate and land-use change scenarios, while the provision of other ES declines. Especially in places where high rates of land-use change are likely to occur, the encroachment of rice and vegetable fields in natural forests not only leads to a reduction in carbon storage but also reduces potential timber and firewood extraction and affects habitats for plant and animal species. These findings demonstrate that not only the impacts of climate and land-use change alone but also the synergies and trade-offs among associated ES have to be considered to develop viable strategies for sustainable management of agro-ecosystems under environmental and anthropogenic pressure (Langerwisch et al. 2018).

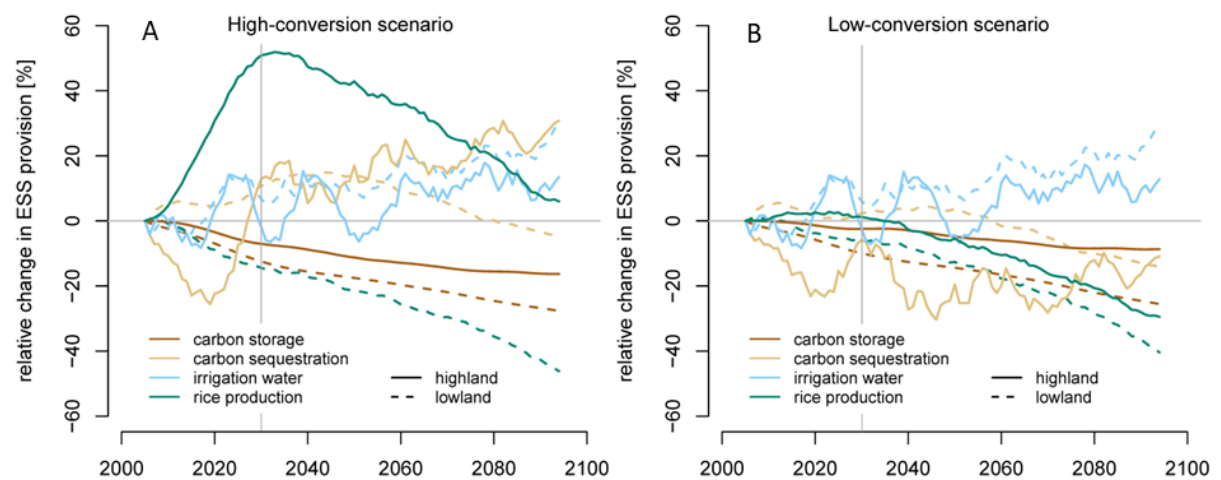


Figure 10. Time series of combined effects of climate and land use change on the provision of four ecosystem services (compared to the baseline period 2001 to 2010) under the SRES scenario A2. The panel shows ESS dynamics for (A) High-conversion and (B) Low-conversion land change scenario. Grey line indicates the last year of the land-use change scenarios. Adapted from Langerwisch et al. (2018).

4 Local-scale dimensions of human–environment interactions

4.1 Quantifying local landscape heterogeneity

The need to quantify landscape heterogeneity has been driven by the landscape ecological paradigm that ecological or anthropogenic processes can be implied and predicted from the spatial pattern of landscape features (Pickett and Cadenasso 1995). Numerous examples why such knowledge is important include understanding landscape changes through time, comparing two or more different landscapes, or evaluating alternative landscape patterns that result from different land use and land management strategies (Rindfuss et al. 2004, Turner 2005). Data, approaches and methods that allow quantifying landscape heterogeneity and linking them to ecological processes are thus central to modern landscape ecology (Wu and Hobbs 2002, Kupfer 2012).

The application of landscape metrics to GIS and remote sensing data is considered as relatively simple, effective approach for assessing and monitoring changes in landscape heterogeneity and their effects on underlying ecological processes (Li and Wu 2004, Levin 2011).

Landscape metrics are numerical indices that describe either compositional or configurational aspects of landscape structures based on data from analog or digital maps derived from remotely sensed images. In these data, landscape heterogeneity is defined in the form of discrete patches, while landscape pattern is described using metrics that quantify patch-level characteristics (e.g. size, shape, isolation) and landscape-level properties (e.g. patch richness, landscape diversity, landscape connectivity) (McGarigal 2002). However, several studies raised the concern that the ecological relevance of many metrics (i.e. the relationship between metric values and the real-world ecological processes) is not always proven by empirical testing, and that such metrics fail to capture important aspects of landscape function (Li and Wu 2004, Kupfer 2012).

Alternative approaches that would incorporate functional components into existing landscape metrics have been advocated to better link landscape pattern with the ecological function of landscapes (Kupfer 2012, Meentemeyer et al. 2012). Metrics such as ‘core area’ based on defining functional edge buffer or ‘isolation’ based on nearest neighbor distance have been shown as useful predictors of the presence and abundance of area-sensitive species or species dependent on the structural connectivity of landscape features (Fahrig 2000, 2013, Collinge et al. 2003). However, approaches using graph theory (Urban and Keitt 2001) or least-cost path analysis (Adriaensen 2003) are better suited to estimate the functional connectivity of landscape features in the context of dispersal or migration of studied organisms.

For example, in our past research we used the least-cost path analysis to study the establishment and spread of the invasive forest pathogen, *Phytophthora ramorum*, in semi-natural forest landscapes (Ellis et al. 2010, Hohl et al. 2014). Given the passive dispersal of microscopic spores through wind-driven rain or stream flow, which cannot be traced or modelled directly, we applied least-cost path analyses to estimate potential transmission pathways among fragmented patches of host and non-host habitat (Figure 11). Various scenarios of landscape resistance to pathogen transmission were assigned to landscape features based on either the type of habitat (Ellis et al. 2010) or hydrological connectivity (Hohl et al. 2014) and compared against field data on disease occurrence. Both studies showed that after accounting for variations in climate and local environmental conditions the functional landscape and hydrological connectivity is a key predictor of pathogen occurrence and disease severity.

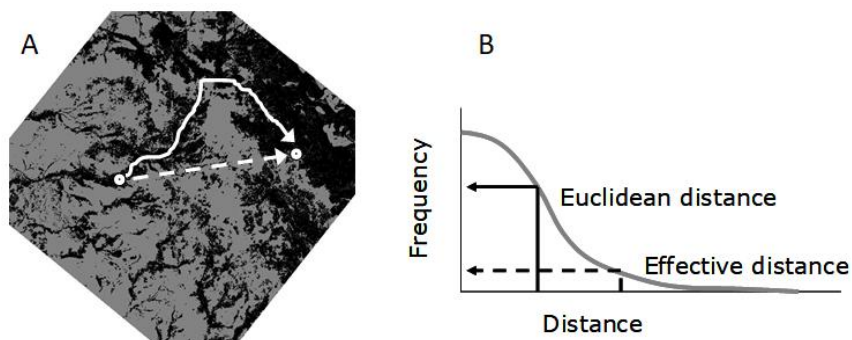


Figure 11. (A) Raster map of host (black) and non-host (gray) habitat for *Phytophthora ramorum* with an example of a Euclidean transmission pathway (dashed line) and a functional transmission pathway (solid line) between two sampling plot locations. (B) Frequency of pathogen spores traveling a given distance based on different estimates of the number of propagules using Euclidean or effective (functional) least-cost path distance. Adapted from Ellis et al. (2010).

4.2 Effects of landscape heterogeneity in agro-ecosystems

Another approach to a more functional quantification of landscape effects is to study how the composition and configuration of landscape features affect functional groups and functional traits of studied biological communities. This was one of the main tasks of the LEGATO project, which aimed at advancing long-term sustainable development of irrigated rice agro-ecosystems in Southeast Asia and developing principles of ecological engineering that would enhance natural mechanisms of biological pest control in these anthropogenic production systems (Settele et al. 2018).

Since rice (*Oryza sativa* L.) is the second most widely grown cereal in the world, continued population growth and increasing demand for food places irrigated rice terraces among the most important agro-ecosystems globally. Man-made rice landscapes in the tropics are also exceptional in the level of biodiversity they harbor, especially in terms of insect species (e.g. more than 640 taxa of macroinvertebrates occur in the Philippine rice fields) (Schoenly et al. 2010). The annual rice production has more than doubled since the beginning of the 'green revolution' in 1960s, but in many areas rice yields are threatened by reoccurring planthopper pest outbreaks (Bottrell and Schoenly 2012). Different strategies are employed to control pest damages, including the use of resistant cultivars, synthetic pesticides or methods of ecological engineering which suppress pests by enhancing the activity of their natural enemies (parasitoids and predatory spiders and bugs) (Gurr et al. 2011). However, extensive pest outbreaks are resurging because the complex interactions between pests, their natural enemies and available habitat resources are poorly understood (Bottrell and Schoenly 2012).

In a series of field studies, we investigated the influence of local landscape heterogeneity and habitat resources on the distribution of different functional groups of arthropods in three rice-production regions in the Philippines and applied these findings to make recommendations for landscape management (Dominik et al. 2017, 2018). First, we described the arthropod community composition at 28 sites in three different regions in the Philippines, using a simple, binary differentiation to quantify landscape heterogeneity (Dominik et al. 2017). All sites were described as either high or low heterogeneity sites, depending on the amount of rice and non-rice habitat within a 100 radius around the sampling locations. We found very limited effect of this fine-scale landscape heterogeneity on assemblage structure (arthropod abundance, species richness or diversity), present only in one region and for two functional groups (predators and detritivores). However, elevation gradient, used as a proxy for regional-scale effects such as climate and land management conditions, explained more than half of variance in assemblage structure. These findings suggested that regional-scale conditions rather than fine-scale landscape heterogeneity explained the composition of rice-arthropod communities and that more sophisticated approaches for quantifying landscape structure are needed to disentangle the complex landscape effects on biocontrol functions.

Therefore, the follow-up study used remotely sensed data on land cover to calculate four independent metrics of landscape composition and configuration within three buffer distances (100, 200 and 300 m radii), and examined how they affect species abundance and species richness of rice arthropods within four arthropod functional groups (Dominik et al. 2018). Functional groups were used here as a suitable descriptor for linking population and ecosystem processes, and for defining the functional differences between herbivores (i.e. pests when at high density),

natural enemies (i.e. predators and parasitoids) and detritivores/tourists (i.e. species that have no direct association with the rice plant but may be attracted from surrounding non-rice habitats). The analyses showed that predator abundances were driven largely by the availability of prey but all other functional groups in the rice-arthropod community were significantly affected by the composition and configuration of surrounding landscape features (Figure 12). Specifically, the pest abundance decreased with increasing landscape diversity (Figure 12a), while the abundance of parasitoids (Figure 12b) and species richness of predators (Figure 12c) increased with the structural connectivity of rice bunds, i.e. the terrestrial levees surrounding and connecting each rice field in the terraced agro-ecosystem. Finally, landscape fragmentation of the rice fields had a clear negative effect on most arthropod groups (e.g. Figure 12d), except for highly mobile predatory arthropods.

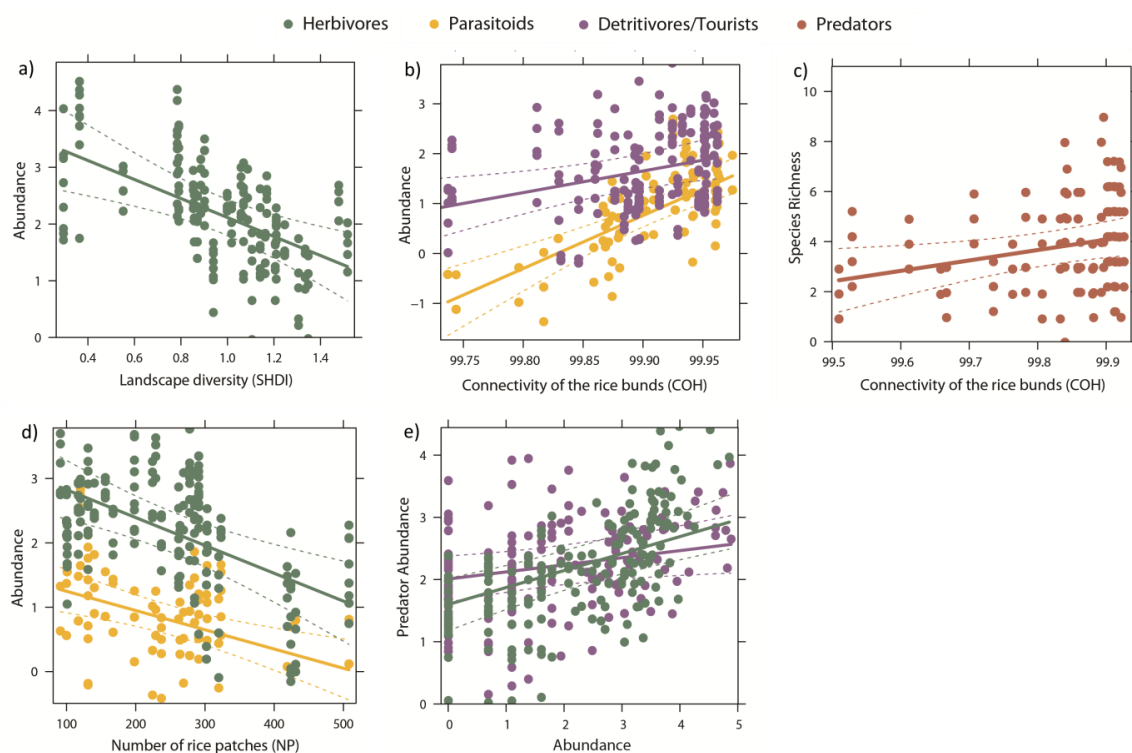


Figure 12. Linear mixed effects models representing relationships between (a) landscape diversity and abundance of herbivores, (b) structural connectivity of the rice bund and abundance of detritivores/tourists and parasitoids, (c) structural connectivity of the rice bunds and species richness of predators, (d) number of rice patches (NP) and abundance of both herbivores and parasitoids, and (e) trophic interactions between predators, herbivores, and detritivores/tourists. All abundance data were log-transformed. Adapted from Dominik et al. (2018).

Although such studies in real agricultural settings have been relatively rare and confined to either tropical rice cropping systems (Wilby et al. 2006, Schoenly et al. 2010, Gurr et al. 2011) or agricultural mosaics in the temperate zone (Steffan-Dewenter et al. 2002, Thies et al. 2003, 2005, Chaplin-Kramer et al. 2011), their findings have specific implications for the management of anthropogenic agro-ecosystems. Although large field sizes are often preferred as they allow the use of mechanization and decrease production costs, diversified agricultural landscapes with

smaller patches and connected non-crop habitat can be beneficial for farmers as they limit the risk of pest outbreaks. In rice agro-ecosystems, higher landscape diversity surrounding rice fields and smaller size of the rice crop patches can result in lower herbivore abundance. Therefore, management practices aiming to improve biodiversity and natural pest control should focus on maintaining smaller rice patches and the structural connectivity of rice bunds to enhance populations of the natural enemies of rice pests (Dominik et al. 2018). In general, this shows that multifunctional landscapes, which promote biodiversity and provide suitable conditions for agriculture but also other ecosystem services, may contribute to the development of productive yet sustainable agricultural systems (Bianchi et al. 2006).

5 Conclusions

Human–environment interactions in the Anthropocene include all forms of land use and land management practices, associated changes in land cover (e.g. cropland expansion or habitat loss), climate and carbon fluxes, as well as the anthropogenic impact on biodiversity, ecosystem functioning, biomass production, agricultural systems and food security (Rounsevell et al. 2012). While considerable progress has been made in understanding these issues, the increasing scale and impact of the growing human population requires a paradigm shift in the way we study and ultimately manage land resources for long-term sustainability (Seppelt et al. 2018).

In this thesis, I used examples from my past and current research to illustrate that (i) humans have different effects on the environment at different spatial and temporal scales, that (ii) everything is spatial in the Anthropocene, and that (iii) landscape ecology (embracing the concepts of land systems and ecosystem services) holds great promise to advance our understanding of the novel ecological patterns and processes that emerge from human–environment interactions.

Landscape ecology, however, works with the key principle that observed ecological and land-use patterns can be used to infer the underlying processes that induced the pattern (Turner 2005). But this key assumption does not hold in complex social-ecological systems of the Anthropocene (Rounsevell et al. 2012). Many development pathways (e.g. agricultural expansion and intensification) arise from multiple drivers (e.g. demand for crops, economic incentives, changes in agricultural suitability) and can lead to the same land-use patterns, while similar processes can cause different patterns (Rounsevell et al. 2012, Verburg et al. 2013). To advance our knowledge beyond the current state of the art, future research in landscape ecology needs to continue be grounded in observation, but at the same time it requires a shift towards combining empirical analysis and spatially explicit modeling to reproduce observed ecological patterns and explain them with ecological and anthropogenic processes that occur in reality. Such an approach will provide better insights into human–environment interactions across multiple spatial scales in a way that may help us predict and mitigate environmental changes that we are likely to face in the future.

6 References

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7 Appendices

- Appendix 1: Václavík, T., S. Lautenbach, T. Kuemmerle, and R. Seppelt. 2013. Mapping global land system archetypes. *Global Environmental Change* 23:1637–1647. **(IF = 10.427)**
- Appendix 2: Václavík, T., F. Langerwisch, M. Cotter, J. Fick, I. Häuser, S. Hotes, J. Kamp, J. Settele, J. H. Spangenberg, and R. Seppelt. 2016. Investigating potential transferability of place-based research in land system science. *Environmental Research Letters* 11:095002 **(IF = 6.192)**
- Appendix 3: Delzeit, R., F. Zabel, C. Meyer, and T. Václavík. 2017. Addressing future trade-offs between biodiversity and cropland expansion to improve food security. *Regional Environmental Change* 17:1429–1441. **(IF = 3.149)**
- Appendix 4: Dittrich, A., R. Seppelt, T. Václavík, and A. F. Cord. 2017. Integrating ecosystem service bundles and socio-environmental conditions – A national scale analysis from Germany. *Ecosystem Services* 28:273–282. **(IF = 5.572)**
- Appendix 5: Dominik, C., R. Seppelt, F. G. Horgan, L. Marquez, J. Settele, and T. Václavík. 2017. Regional-scale effects override the influence of fine-scale landscape heterogeneity on rice arthropod communities. *Agriculture, Ecosystems & Environment* 246:269–278. **(IF = 3.954)**
- Appendix 6: Seppelt, R., M. Beckmann, and T. Václavík. 2017. Searching for Win–Win Archetypes in the Food–Biodiversity Challenge: A Response to Fischer et al. *Trends in Ecology & Evolution* 32:630–632. **(IF = 15.236)**
- Appendix 7: Langerwisch, F., T. Václavík, W. von Bloh, T. Vetter, and K. Thonicke. 2018. Combined effects of climate and land-use change on the provision of ecosystem services in rice agro-ecosystems. *Environmental Research Letters* 13:015003. **(IF = 6.192)**
- Appendix 8: Dominik, C., R. Seppelt, F. G. Horgan, J. Settele, and T. Václavík. 2018. Landscape composition, configuration, and trophic interactions shape arthropod communities in rice agroecosystems. *Journal of Applied Ecology* 55:2461–2472. **(IF = 5.782)**
- Appendix 9: Seppelt, R., P. H. Verburg, A. Norström, W. Cramer, and T. Václavík. 2018. Focus on cross-scale feedbacks in global sustainable land management. *Environmental Research Letters* 13:090402. **(IF = 6.192)**
- Appendix 10: Zabel, F., R. Delzeit, J. Schneider, R. Seppelt, W. Mauser, and T. Václavík. 2019. Global impacts of future cropland expansion and intensification on agricultural markets and biodiversity. *Nature Communications* 10(1):2844. **(IF = 11.878)**

Note:

The ten publications included as appendices provide a selection of my research that contributes to the topics covered in this thesis. For eight of the publications, I served as a first, corresponding or last author, typically being a group leader and project PI who supervised the work. For the two publications where I am not the first, corresponding or last author, I have given significant intellectual input or conducted data analysis. In all cases, I contributed substantially to writing the manuscript.