Palacký University
Olomouc

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.

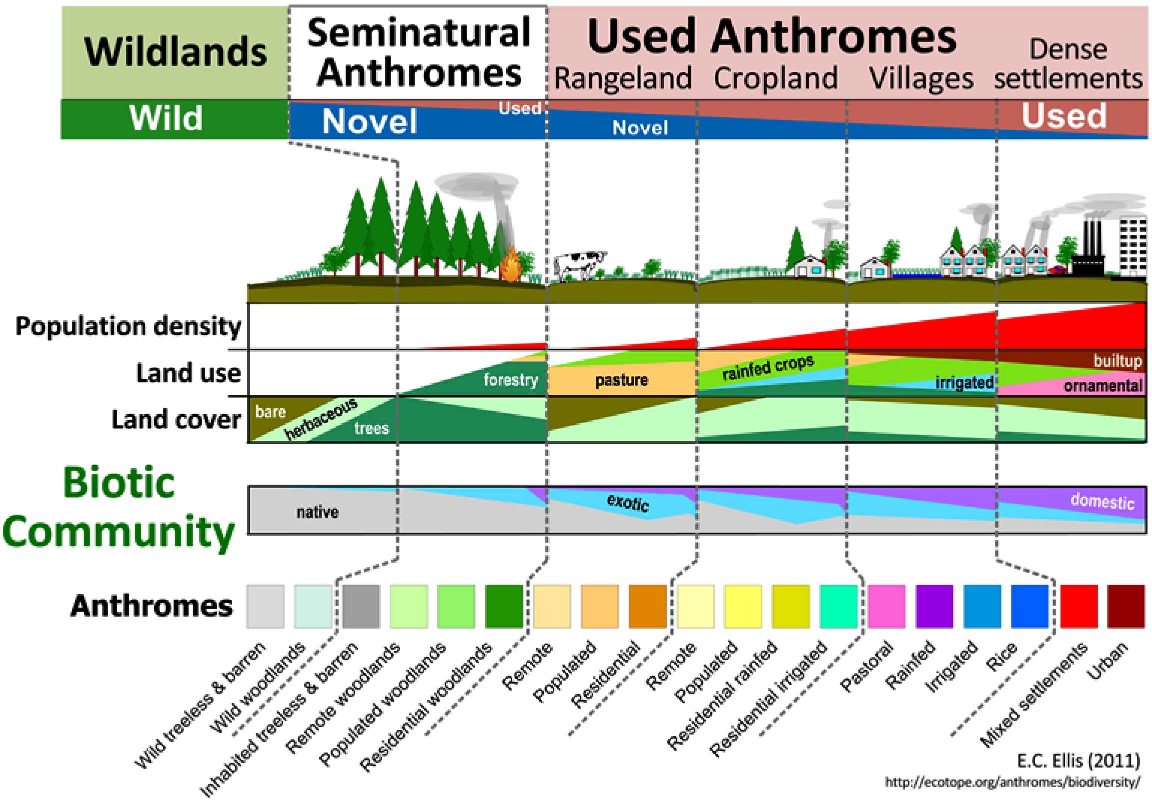

Figure 1. Global anthromes: conceptual framework for anthropogenic transformation of terrestrial biomes. Adopted from Ellis (2011).

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
Land-use intensity factors			
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)
Environmental factors			
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
Socioeconomic factors			
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 archetypical 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).

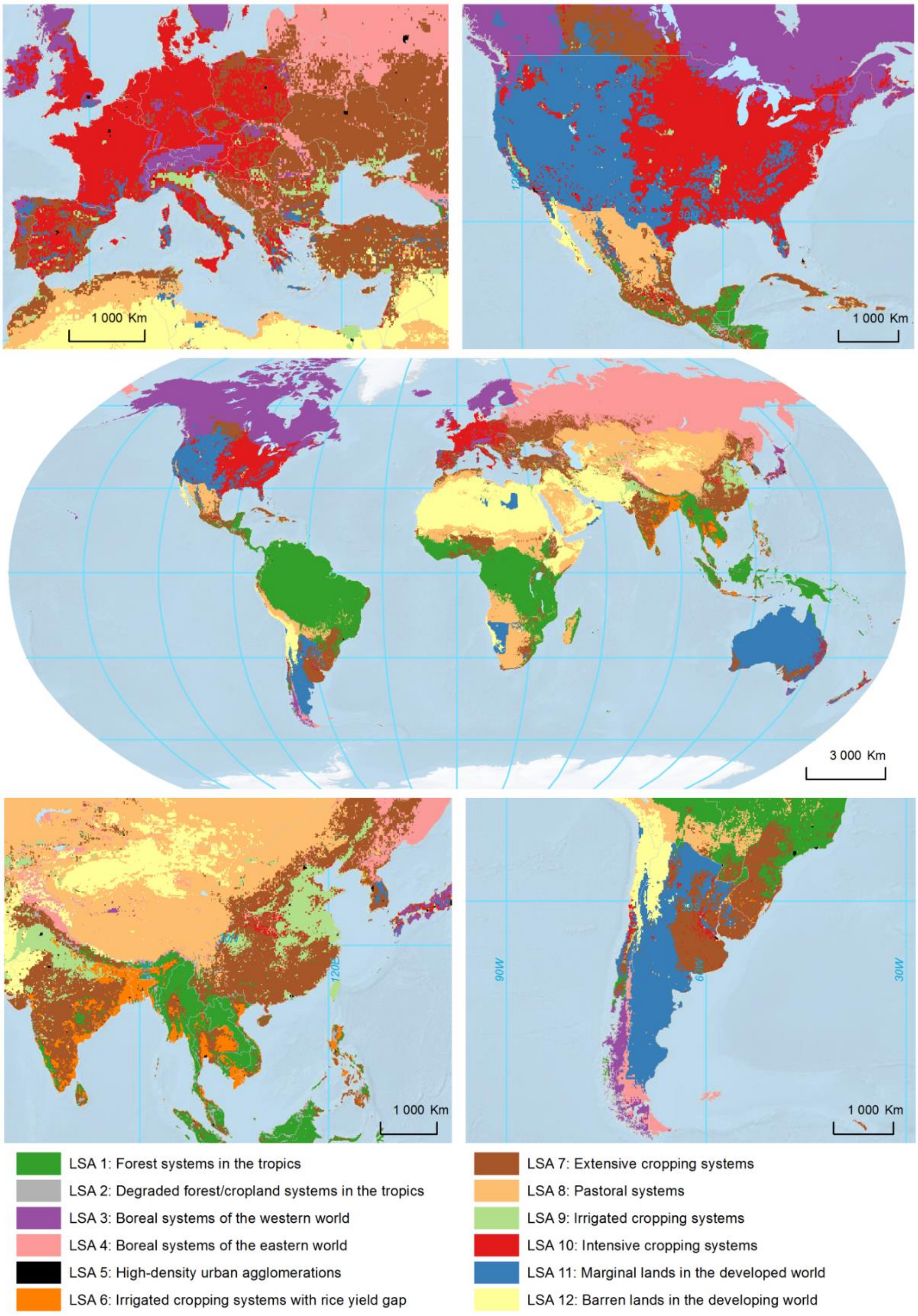

Figure 2. Global land system archetypes; world map and regional areas. Adopted from Václavík et al. (2013).

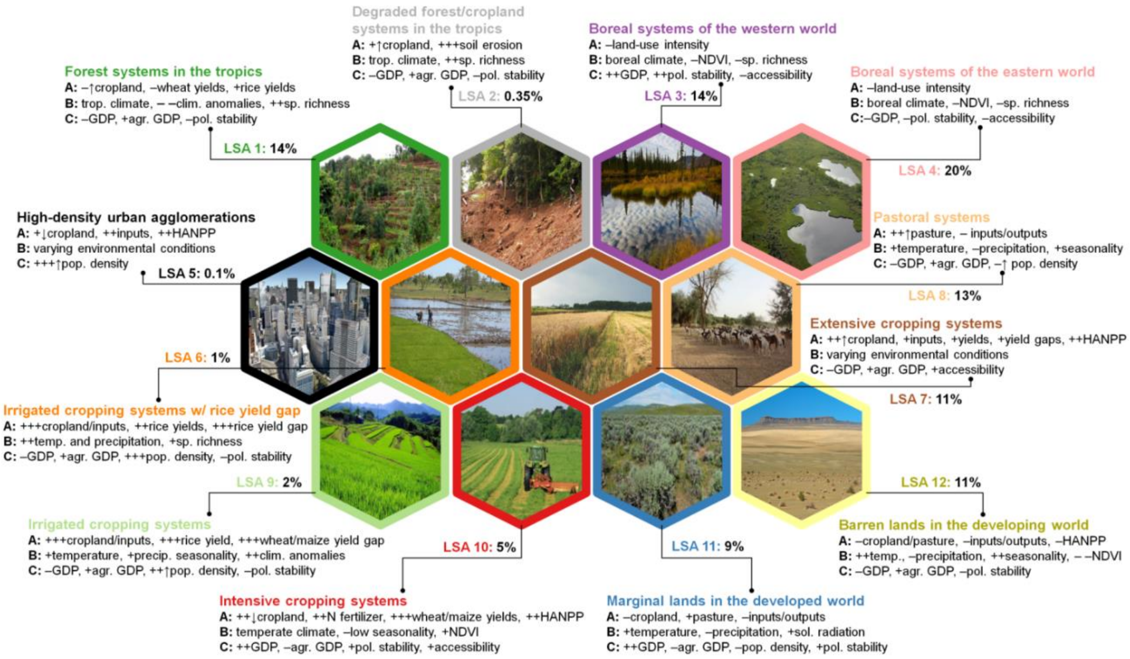

Figure 3. Overview of land system archetypes, summarizing major land-use intensity indicators (A), environmental conditions (B) and socio-economic factors (C) that best characterize each archetype (for list of variables see table 1). The + and – signs show whether the factor is above or below global 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:

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

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/).

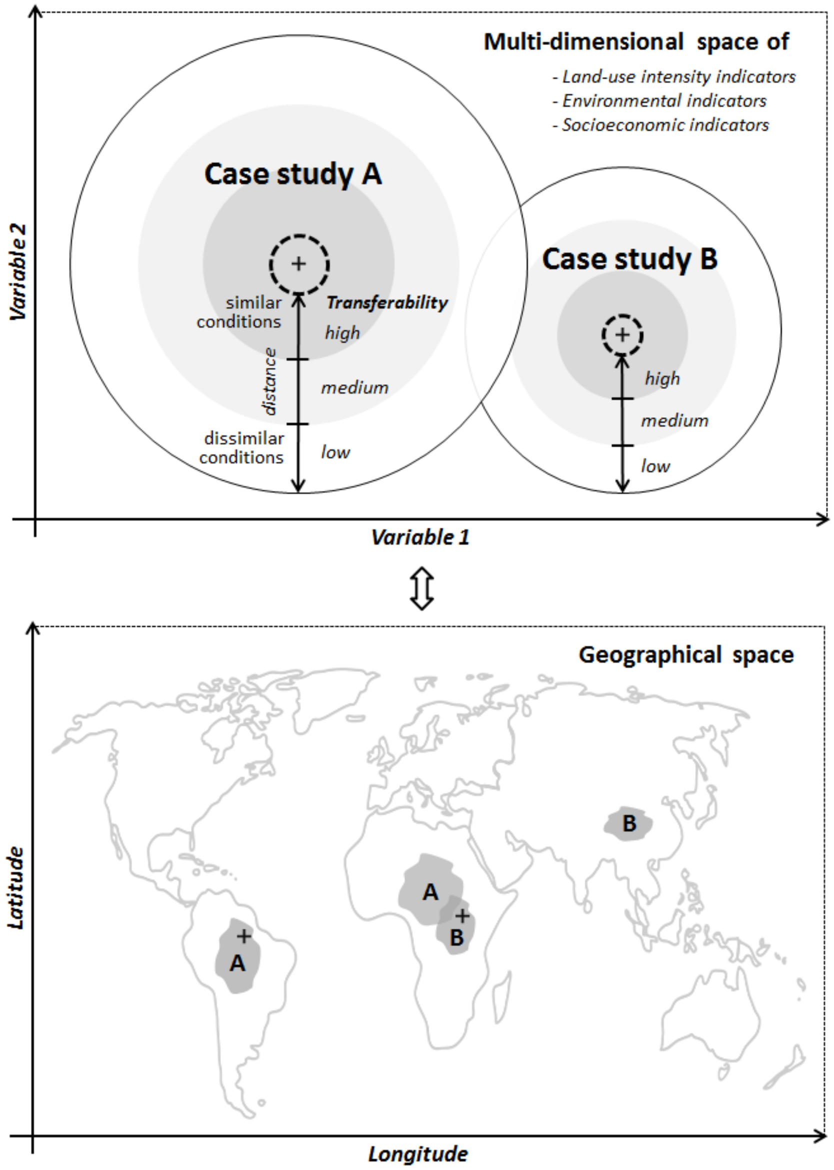

Figure 4. Conceptual diagram of mapping potential transferability of place-based research. The upper rectangle represents a multidimensional space defined by land-use intensity, environmental and socio-economic indicators. The crosses denote the ‘case study archetypes’, i.e. the mean conditions in the 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.

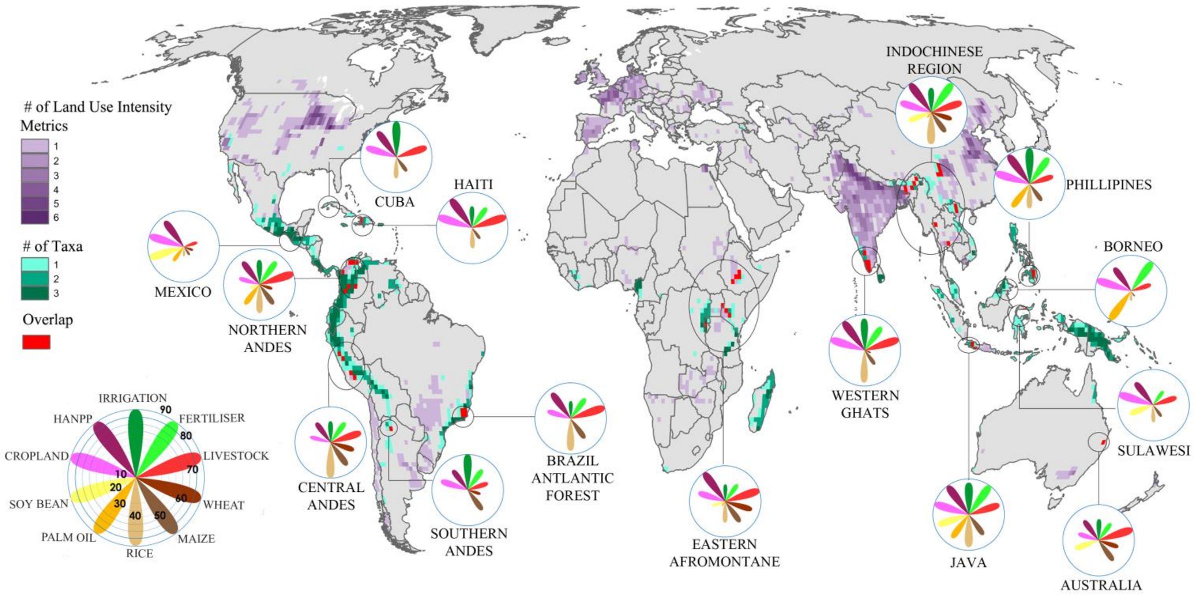

Figure 5. Top 2.5% of current land-use intensity (LUI) and biodiversity, where any of the top 2.5% intensity metric overlaps with any of the top 2.5% of endemism richness for mammals, birds and amphibians, thus highlighting regions of particularly high pressure between human activity and wildlife. Multiple 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).

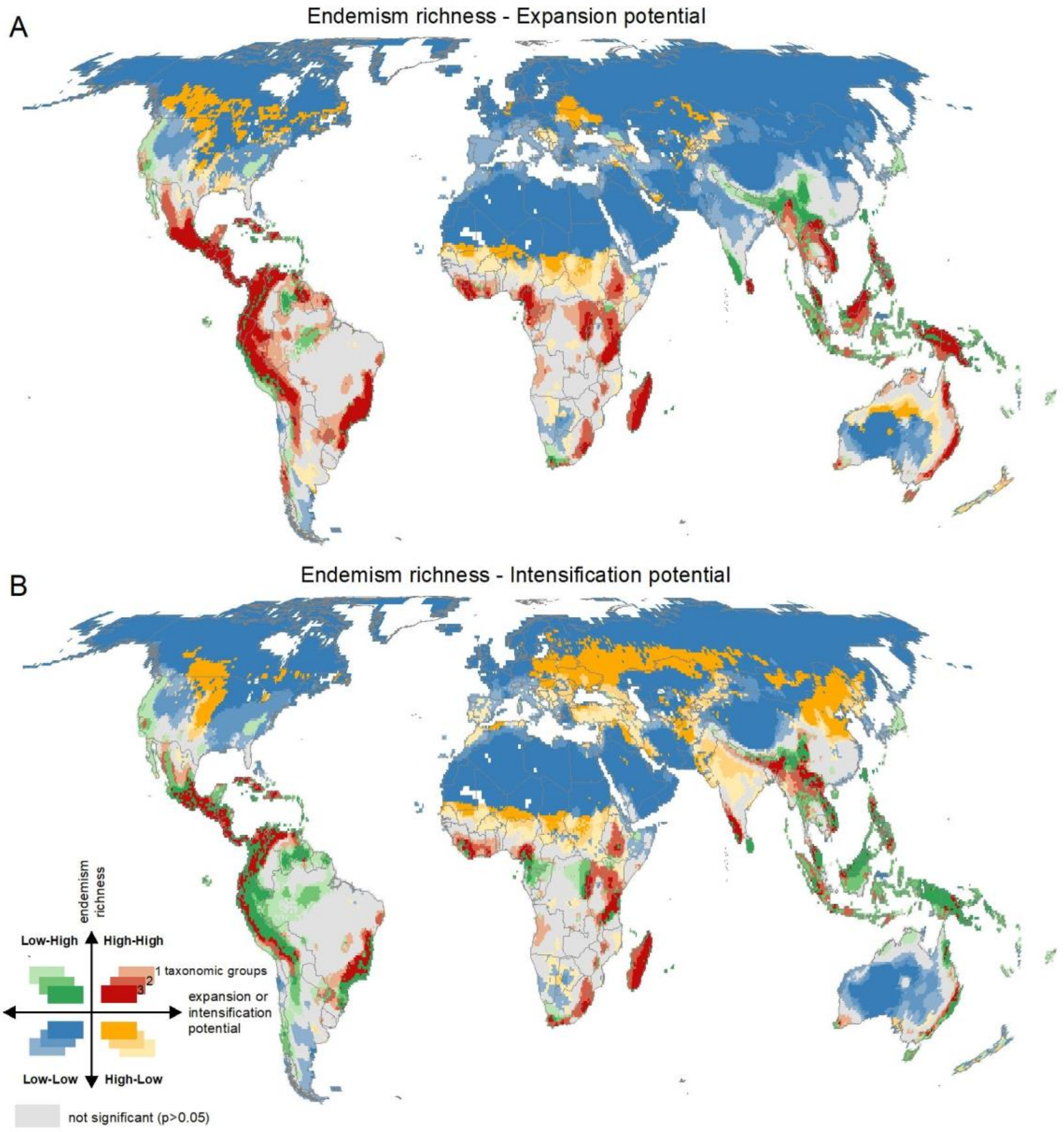

Figure 6. Spatial association between endemism richness and potentials for future (A) cropland expansion and (B) intensification calculated using local indicators of spatial association (LISA) at 55-km resolution. High–high clusters indicate hotspot locations (red), in which areas most suitable for expansion/intensification 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).

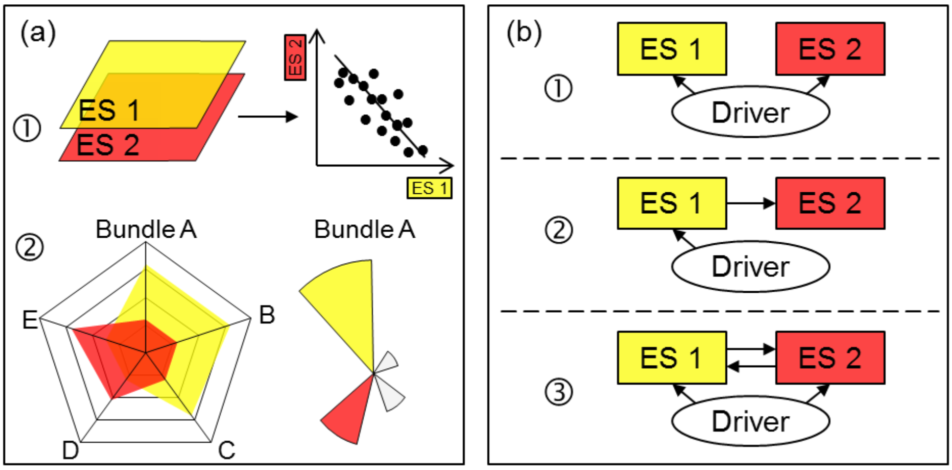

Figure 7. Main goals of studies on ES relationships. (a) Identifying and describing ES co-occurrences: ① Spatial overlay of ES maps and correlation analysis, ② Illustration of ES bundles using spider diagrams (showing multiple bundles A-E) or flower plots (for bundle A); (b) Identifying drivers, environmental 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.

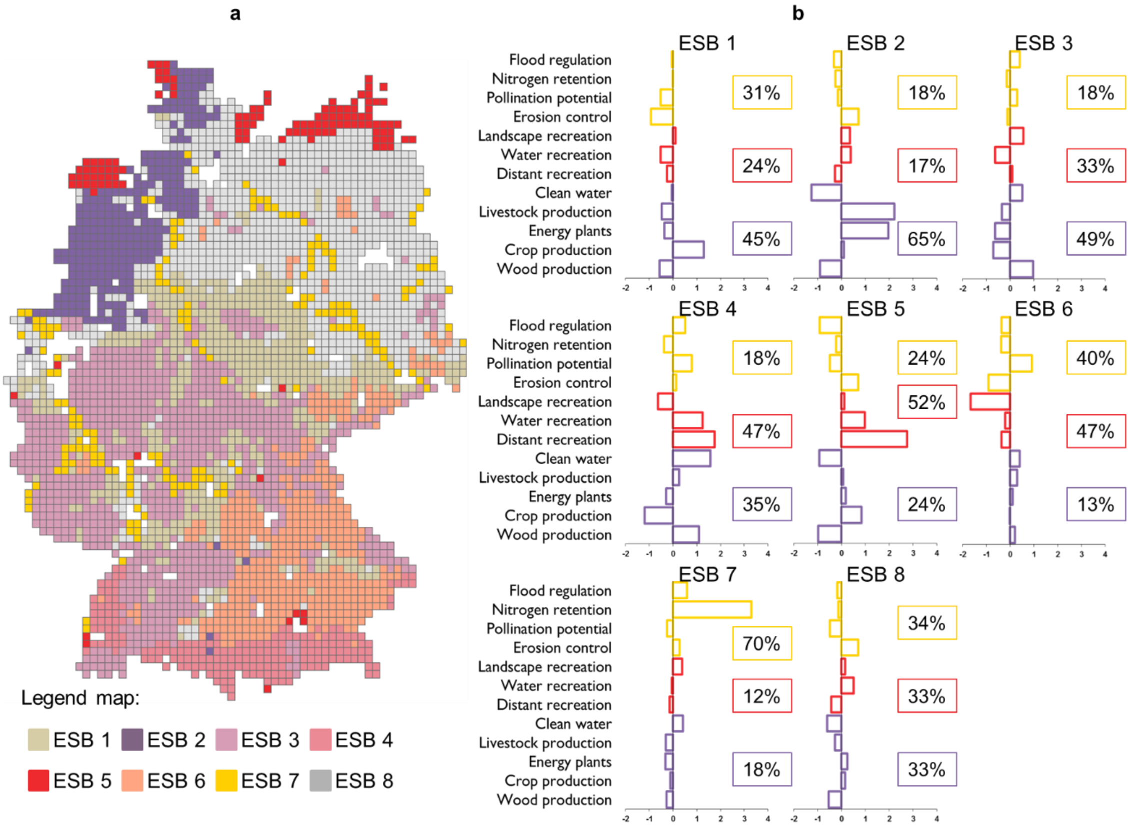

Figure 8. Ecosystem service bundles mapped in Germany (a). The bar plots (b) show the z-score normalized values of ES indicators that best characterize each bundle, with zero representing the national average. The relative contribution of the three ES categories to each bundle is indicated by the percentages 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.

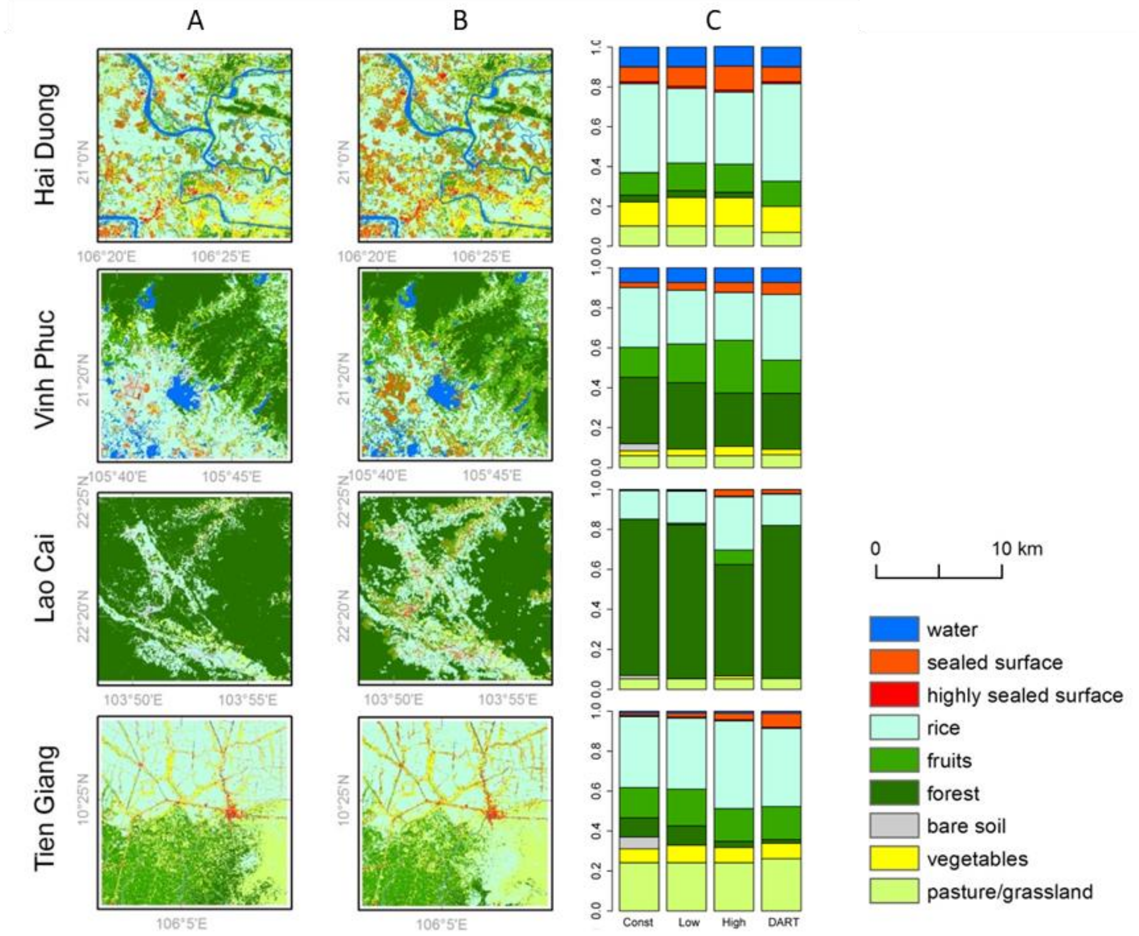

Figure 9. Land use classes in four study areas in Vietnam. (A) Observed land use class, (B) land use in 2030 in the High-conversion scenario and (C) fraction of land use categories in 2030 in all land use change scenarios (Low-conversion, High-conversion and DART). The land use scenario 'Const' refers 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).

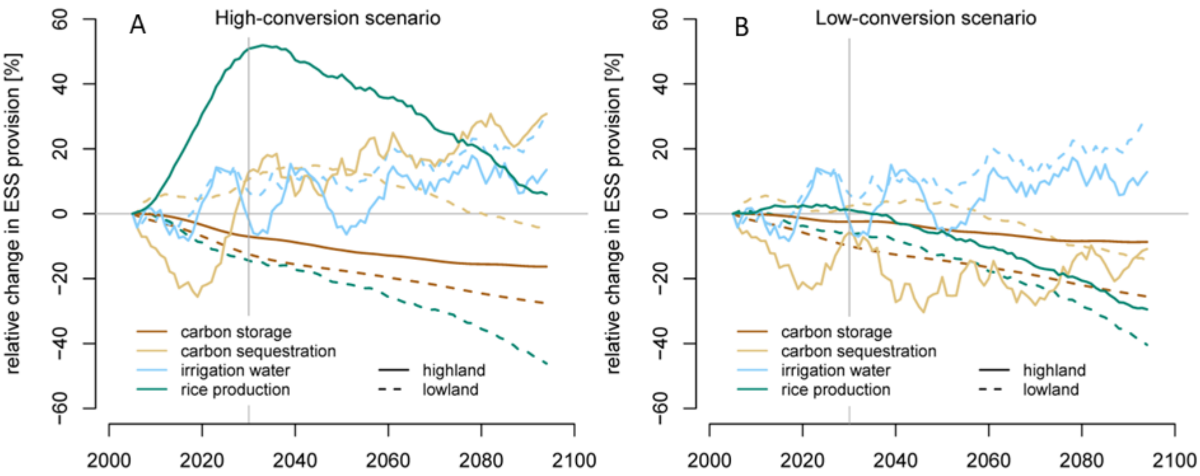

Figure 10. Time series of combined effects of climate and land use change on the provision of four ecosystem services (compared to the baseline period 2001 to 2010) under the SRES scenario A2. The panel shows ESS dynamics for (A) High-conversion and (B) Low-conversion land change scenario. Grey line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

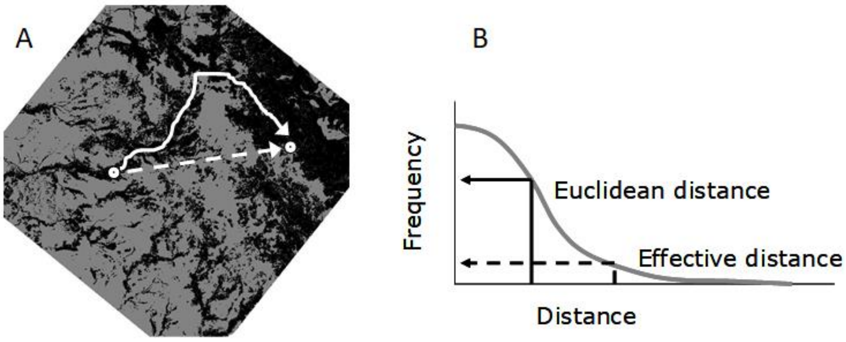

Figure 11. (A) Raster map of host (black) and non-host (gray) habitat for *Phytophthora ramorum* with an example of a Euclidean transmission pathway (dashed line) and a functional transmission pathway (solid line) between two sampling plot locations. (B) Frequency of pathogen spores traveling a given 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 detritivors). 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.

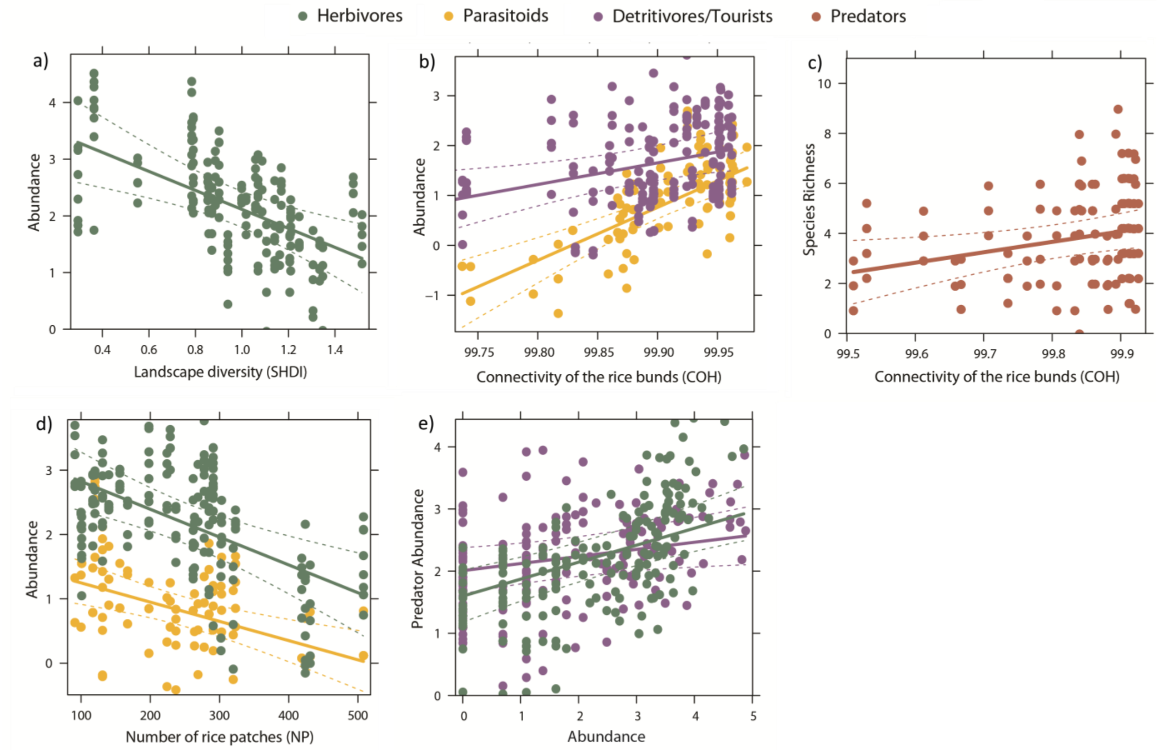

Figure 12. Linear mixed effects models representing relationships between (a) landscape diversity and abundance of herbivores, (b) structural connectivity of the rice bund and abundance of detritivores/tourists and parasitoids, (c) structural connectivity of the rice bunds and species richness of predators, (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.

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Appendix 1

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Mapping global land system archetypes

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ABSTRACT

Land use is a key driver of global environmental change. Unless major shifts in consumptive behaviours occur, land-based production will have to increase drastically to meet future demands for food and other commodities. One approach to better understand the drivers and impacts of agricultural intensification is the identification of global, archetypical patterns of land systems. Current approaches focus on broad-scale representations of dominant land cover with limited consideration of land-use intensity. In this study, we derived a new global representation of land systems based on more than 30 high-resolution datasets on land-use intensity, environmental conditions and socioeconomic indicators. Using a self-organizing map algorithm, we identified and mapped twelve archetypes of land systems for the year 2005. Our analysis reveals similarities in land systems across the globe but the diverse pattern at sub-national scales implies that there are no 'one-size-fits-all' solutions to sustainable land management. Our results help to identify generic patterns of land pressures and environmental threats and provide means to target regionalized strategies to cope with the challenges of global change. Mapping global archetypes of land systems represents a first step towards better understanding the global patterns of human–environment interactions and the environmental and social outcomes of land system dynamics.

1. Introduction

Not only is the world experiencing rapid changes in climate and biodiversity patterns, but increasing consumption of goods and services is placing an enormous pressure on natural ecosystems and the resources they harbour (Butchart et al., 2010; Foley et al., 2005). Particularly, land use has become a major driver of global change because human populations drastically alter land in order to satisfy their basic needs for food, fibre, energy and housing. Human utilization of the biosphere has reached such a magnitude that now more than 75% of ice-free land shows evidence of marked human alteration (Ellis and Ramankutty, 2008) and almost 30% of global terrestrial net primary production is appropriated for human use (Haberl et al., 2007). Current land-use practices result in changes in the Earth's biogeochemical cycles and ultimately in the ability of ecosystems to deliver services critical to human well-being (MEA, 2005). 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).

Land-based agricultural production is expected to increase further to meet future demands for food and other commodities, such as biofuel or fibre (Kearney, 2010; Kiers et al., 2008). However, as fertile land resources are getting scarcer and ecosystem functions and services degraded, further agricultural expansion becomes hardly acceptable. Future production increases will have to be, to a large part, achieved via intensifying existing production systems in order to reach global food security and environmental sustainability (Tilman et al., 2011, 2002). Whereas the distribution of agricultural expansion is relatively well mapped (DeFries et al., 2010; Klein Goldewijk, 2001; Klein Goldewijk et al., 2011; Ramankutty et al., 2008, 2002), the patterns of land-use intensity remain poorly understood at the global scale. To identify the potential for sustainable intensification and to better understand the environmental and

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social trade-offs, constraints, and opportunities connected to it, we urgently need to move beyond mapping broad agricultural classes towards mapping land use systems (DeFries and Rosenzweig, 2010).

Traditional models of land systems focus on broad-scale representations of land cover with limited consideration of human influence or land-use intensity (GlobCover, Arino et al., 2007; GLC 2000, Bartholome and Belward, 2005). 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 intensity. Mapping land systems, and thereby incorporating the multidimensional aspects of land-use intensity and land management practices, can help us to (i) better understand the interactions and feedbacks among different biophysical and social components, (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), (iii) address global trade-offs and distant impacts of land-use change (Seppelt et al., 2011), and (iv) develop better policies and spatially explicit solutions adapted to regional conditions (Foley et al., 2011). These efforts require a global analysis of land systems that would help identify both the intensity and geographical manifestation of human–environment interactions.

Several new studies made critical strides towards better integrating land management patterns in global representations of the earth's surface. For instance, Ellis and Ramankutty (2008) suggested a new classification of anthropogenic biomes as an innovative view of the human-dominated biosphere. These anthromes are 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. Most recently, 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 wheat, maize and rice. These studies used either indirect or a few direct indicators of land-use intensity. They also applied top-down approaches to define land system classes based on expert's rules or a priori classification. To complement these efforts and reduce the level of subjectivity in the classification, an alternative approach is needed that would account for the multiple dimensions of land-use intensity and provide a typology of land systems driven mostly by data rather than by predefined assumptions. Such analysis may help us better understand the global patterns of human–environment interactions and land use intensity and examine the social and environmental outcomes of land system dynamics.

In this study, we propose a new approach for representing human–environment interactions as global archetypes of land systems, which we define as unique combinations of land-use intensity, environmental conditions and socioeconomic factors, with patterns that appear repeatedly across the terrestrial surface of the earth. We aim to move beyond the abovementioned representations by explicitly addressing the multidimensional aspects of land-use intensity and both the drivers of land use and its impacts. Our analysis takes advantage of globally continuous, high spatial resolution datasets on more than 30 indicators of land systems and adopts a bottom-up approach driven solely by the data. We hypothesize that (1) land systems can be clustered in consistent groups based on the similarity of available indicators of global land-use and that (2) the same land system archetypes (LSAs) can be identified across the globe, while diverse patterns can be found at the sub-national scale. By mapping LSAs, we offer a broad view of the most relevant characteristics of human–environment interactions while still preserving local context

Table 1
Datasets used for classification of land system archetypes.

Archetype factor	Spatial resolution	Unit	Source
Land-use intensity factors			
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)
Environmental factors			
Temperature	10 arc-minutes	°C × 10	Kriticos et al. (2012)
Diurnal temperature range	10 arc-minutes	°C × 10	Kriticos et al. (2012)
Precipitation	10 arc-minutes	mm	Kriticos et al. (2012)
Precipitation seasonality	10 arc-minutes	Coeff. of variation	Kriticos et al. (2012)
Solar radiation	10 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	Batjes (2006)
Species richness	Calculated from range polygons	# of species per grid cell	http://www.iucnredlist.org/technical-documents/spatial-data
Socioeconomic factors			
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 (2005)
Population density trend	2.5 arc-minutes	$persons\,km^{-2}$	CIESIN (2005)
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

needed for place-specific solutions to global challenges of land use and sustainability.

2. Materials and methods

2.1. Data sources and preparation

Global patterns of land system archetypes were identified based on 32 indicators characterizing land-use intensity (covering input and output intensity factors), environmental factors and socioeconomic factors (Table 1). We hypothesized these variables would well represent the multidimensional aspects of human–environment interactions, while many of these factors function both as drivers and consequences in the complex land systems. While some variables were not completely independent from each other, as they were created by a combination of several datasets or models, we inspected Pearson correlations between all variables to avoid redundancy in the input information (Table A1). Our final set of input data included only those variables with $|r| < 0.7$ (Dormann et al., 2013). All datasets on the current land-use status were derived for the period around the year 2005 and were aggregated prior to the analysis to 5 arc-minutes ($\sim 9.3 \times 9.3$ km at the equator) spatial resolution. In addition, we included several indicators of temporal trends to account for legacies and transient dynamics of LSAs. The Arctic and Antarctic regions were excluded from the analysis.

2.1.1. Land-use intensity factors

Land-use intensity is a multidimensional issue and we therefore used indicators that characterize land-use intensity in terms of inputs, outputs and system properties (Kuemmerle et al., 2013). Data on cropland and pasture cover were obtained from the HYDE 3.1 database (Klein Goldewijk et al., 2011), an updated version of the standard data source for investigations of human-induced land change (Ellis et al., 2010; Hurtt et al., 2006). The HYDE model combines agricultural statistics with remote sensing data and allocation algorithms to produce spatially explicit maps of agricultural intensity (Klein Goldewijk, 2001; Klein Goldewijk et al., 2011). In addition to the status for 2005, we included temporal trends in cropland and pasture densities over the last 50 years. These trends were calculated as the difference between the values in 2005 and 1955, so the variables describe overall increase or decrease of the factors in the 50-year period. The amount of fertilizer applied and area under irrigation were used as additional indicators of land-use intensity. We acquired spatially explicit estimates of nitrogen (N) and phosphorus (P) inputs resulting from global fertilizer application and manure production (Potter et al., 2010). We used only the N fertilizer variable in the final analysis due to its high correlations with P fertilizer (Pearson correlation > 0.9). Irrigation data were obtained from the Global Map of Irrigation Areas version 4.0.1 which shows the area equipped for irrigation estimated by combining subnational statistics with geospatial information on the position and extent of irrigation schemes (Siebert et al., 2007). As large-scale soil erosion is a major consequence of industrial agriculture and an indicator of land degradation (Boardman, 2006), we also acquired data from Van Oost et al. (2007) who simulated global distribution of soil erosion caused by water and tillage. The estimates were based on mechanistic models that quantitatively described the relationship between sediment erosion and land use, topography, climate and soils as controlling factors.

As an indicator of the intensity and efficiency of land-based production, we acquired data on yields and yield gaps for wheat, maize and rice from the GAEZ v3.0 database (IIASA/FAO, 2012). These data were developed by downscaling the national and subnational crop production statistics (Monfreda et al., 2008) and allocating them to cultivated land. Yields were calculated for both rain-fed and irrigated croplands in t ha^{-1} year^{-1} and yield gaps represented the difference between actual production and potential agro-ecological productivity. We also included one country-level indicator of land-based production: the total production index (TPI) which represents the relative level of the aggregate volume of agricultural production in comparison with the base period 1999–2001. As an additional indicator of land-use intensity and human pressure on land, we used data on the human appropriation of net primary production (HANPP) that represents an aggregate impact of land use on biomass available in ecosystems (Haberl et al., 2007). HANPP accounts not only for biomass withdrawn from ecosystems through harvest but also for NPP losses due to biomass being destroyed during harvest and due to decreased productivity of human-dominated ecosystems as compared to productivity of natural ecosystems (Erb et al., 2009).

2.1.2. Environmental factors

Global patterns of land-use forms and processes are constrained by climate and other biophysical attributes that represent the system as a whole. To represent climate, we mapped annual means of 35 bioclimatic variables derived from the CliMond database (Kriticos et al., 2012). These interpolated surfaces were calculated from the original WorldClim variables (Hijmans et al., 2005) as historical climate averages centred on 1975. For the final analysis, we selected five bioclimatic factors with low correlation (<0.6) to avoid redundant information in the dataset (Table 1). In addition, we mapped mean climate anomalies reflecting 10 years (2001–2010) of anomalies in land surface temperatures measured by NOAA's Global Historical Climatology Network (Menne et al., 2009). Because the 5° aggregated data contained missing values, we interpolated them with thin plate spline algorithm (Hutchinson, 1995) to obtain global coverage. To account for biophysical factors that reflect the productivity of ecosystems, we calculated the mean and standard deviation (seasonality) of the normalized difference vegetation index (NDVI) acquired from the Global Inventory Modelling and Mapping Studies (GIMMS) available for a 25 year period spanning from 1981 to 2006 (Tucker et al., 2005). NDVI has been used extensively for investigations of global change because it correlates with primary productivity of ecosystems and is an indicator of vegetation cover and land-use practices (DeFries and Townshend, 1994; Lunetta et al., 2006; Pettorelli et al., 2005). As soil is a crucial physical constraint for plant growth and crop production (FAO, 1999), we included data on soil organic carbon from the ISRIC–World Soil Information project (Batjes, 2006). Finally, we included a measure of species diversity because biodiversity reflects both natural conditions and long-term effects of land management (Ewers et al., 2009; Green et al., 2005; Phalan et al., 2011). For the taxonomic groups of terrestrial mammals, birds, reptiles and amphibians, we obtained global range polygon data from the International Union for Conservation of Nature (IUCN) database and used overlay analysis to calculate species richness (number of species) for each grid cell.

2.1.3. Socioeconomic factors

As economic indicators of land systems, we used three statistical indices provided by the Food and Agriculture Organization (FAO) at a national level. Gross domestic product (GDP) represents the market value of all officially recognized goods and services produced within a country, and GDP from agriculture indicates the proportion of an economy's total domestic output resulting from the agricultural sector. The capital stock in agriculture quantifies investments and physical assets used in the production process covering land development, irrigation works, structures, machinery and livestock. As broad indicators of the degree of human impact on land, we used gridded data on globally consistent estimates of population density (CIESIN, 2005). Similar to the case of cropland and pasture areas, we used the status for 2005 but also calculated changes in global population density for the last 50 years. For socioeconomic indicators, we used the worldwide governance indicators (WGI) and market accessibility. WGI reports on six dimensions of a country's governance, including voice and accountability, political stability, government effectiveness, regulatory quality, rule of law and control of corruption (Kaufmann et al., 2010). We chose only one index, political stability, to represent governance indicators in the final classification, in order to avoid multicollinearity in the data. Finally, we used the global map of accessibility that measures travel time to major cities and market places (Uchida and Nelson, 2009). This dataset developed by the European Commission and the World Bank captures connectivity and concentrations of economic activities which are critical drivers of human interactions with the global environment (Verburg et al., 2011a).

2.2. Archetype classification

We adopted a multidimensional classification procedure that explicitly considers the complexity of land-use intensity to examine how this phenomenon manifests itself at a global scale. Hierarchical clustering has been previously used to delineate land cover and farming systems (FAO, 2011; Kruska et al., 2003; Letourneau et al., 2012; van Asselen and Verburg, 2012; van de Steeg et al., 2010) but these approaches required expert rules or supervised threshold selection and used relatively few variables in order to keep the interpretation of classification trees manageable. We used a self-organizing map (SOM) algorithm, an unsupervised neural network, that allows both (i) visualizing complex data sets by reducing their dimensionality and (ii) performing cluster analysis by grouping observations (grid cells in a map) into exclusive sets based on their similarity (Skupin and Agarwal, 2008). SOM is especially useful for the classification of archetypes because our exploratory aim is geared towards uncovering relevant patterns in land systems rather than confirming existing hypotheses. Also, the method preserves topology based on distances (similarity) among input vectors in the two-dimensional output space. If two high-dimensional clusters are very similar, then their position in the two-dimensional space should be very similar (Spielman and Thill, 2008).

The SOM analysis was conducted in R version 2.14.0 (R Development Core Team, 2011) using the package kohonen (Wehrens and Buydens, 2007). First, we prepared training data by randomly sampling all 32 variables with one million data points, in order to decrease the computational burden and reduce spatial autocorrelation in the variables. Second, we checked data for extreme outliers or skewed distributions. Because of their differing units, we normalized all variables by scaling them to zero mean and unit variance. This z-score normalization was important, as it allowed the results to be interpreted in terms of how much and in which direction the characteristic factor in each archetype deviates from the global average. Third, we selected the size and type of the two-dimensional output space. We chose a 3 by 4 hexagonal plane to provide high generalization of clusters required for the purpose of our analysis, while maintaining sufficient links among units in the neural network (for details see Skupin and Agarwal, 2008). We based our choice on a sensitivity analysis that compared different sizes and shapes of SOM output planes, ranging from 2 by 2 to 10 by 10 clusters. For each possible combination, we calculated the mean distance of samples to the codebook vector (see below) of that cluster to which the samples were assigned, normalized by the number of clusters (Wehrens and Buydens, 2007). We identified a natural break in the mean distance for the 3 by 4 SOM size, suggesting a useful trade-off between the number of clusters and their quality of data representation.

The final pattern was identified through an iterative self-organizing process which represents the core of the SOM analysis. During this process, individual input vectors were presented to the output units, the best-matching units were found and the weights of the winning and neighbouring units repeatedly modified until the algorithm converged (Skupin and Agarwal, 2008). To analyze the spatial manifestation of identified clusters, we mapped all samples back to the geographical space and created the final map of LSAs by assigning each grid cell a cluster value of its closest sample point. We evaluated the quality of the classification procedure by calculating the distance of each grid cell, mapped to a particular cluster, to the codebook vector of that cluster (i.e. the combination of variable values that best characterizes the particular cluster). A good classification should show relatively small distances for most locations in the map (Wehrens and Buydens, 2007).

3. Results

The final map of global land system archetypes revealed a clustered pattern of human–environment interactions and land-use intensity (Fig. 1). Each archetype was characterized by a specific combination of land management indicators and its spatial position in the SOM indicated its relation (similarity) to other archetypes (Fig. 2 and Fig. A2). The non-standardized values of land system determinants that best characterize each archetype were summarized in Fig. 3 and Table A2.

Forest systems in the tropics cover approximately 14% of terrestrial ecosystems and are determined mainly by climate conditions, namely high temperature and precipitation, which naturally correspond with primary production that is the highest among all archetypes and supports high species richness (201 species of selected taxonomic groups per grid cell). The climate conditions, however, have experienced most pronounced temperature anomalies in the recent decade. While the cropland and pasture densities are close to the global average (5 and 15% of cover, respectively), their extent has expanded in the last 50 years as a result of continuing deforestation (by 2 and 5 km^2 per grid cell, respectively). Yields for wheat, maize and rice, however, remain below 1 t ha^{-1} $year^{-1}$. These regions have low average GDP (2011 $ per capita) but 18% of their national GDP comes from the agricultural sector. The population density varies substantially from place to place but most of the regions exhibit low political stability. These regions occur in Latin America and the Amazon basin, Central and West Africa, and in Southeast Asia.

Degraded forest/cropland systems in the tropics cover only 0.35% of terrestrial ecosystems but represent areas with the highest estimated soil erosion in the world (120 Mg ha^{-1} $year^{-1}$). This LSA exhibits a scattered pattern in locations where tropical forest had been converted to croplands with the average cropland cover of 25% that increased by 22 km^2 per grid cell in the last 50 years. Although the input of N fertilizer is approximately 9 kg ha^{-1}, the yields of the three major crops are relatively low. However, more than 39% of the net primary production is appropriated for human use. These areas have environmental and socioeconomic conditions highly similar to the forest system archetype and occur especially in Southeast Asia and Latin America.

Boreal systems of the western world (14% of terrestrial ecosystems) consist of a mixture of boreal forests and tundra. The archetype is determined by a combination of boreal climate and low human impact but advanced socioeconomic conditions. The average cover of cropland and pasture is about 6% and both indicators experienced a decreasing trend in the last 50 years. Agricultural intensity is very low with minimal potential for higher

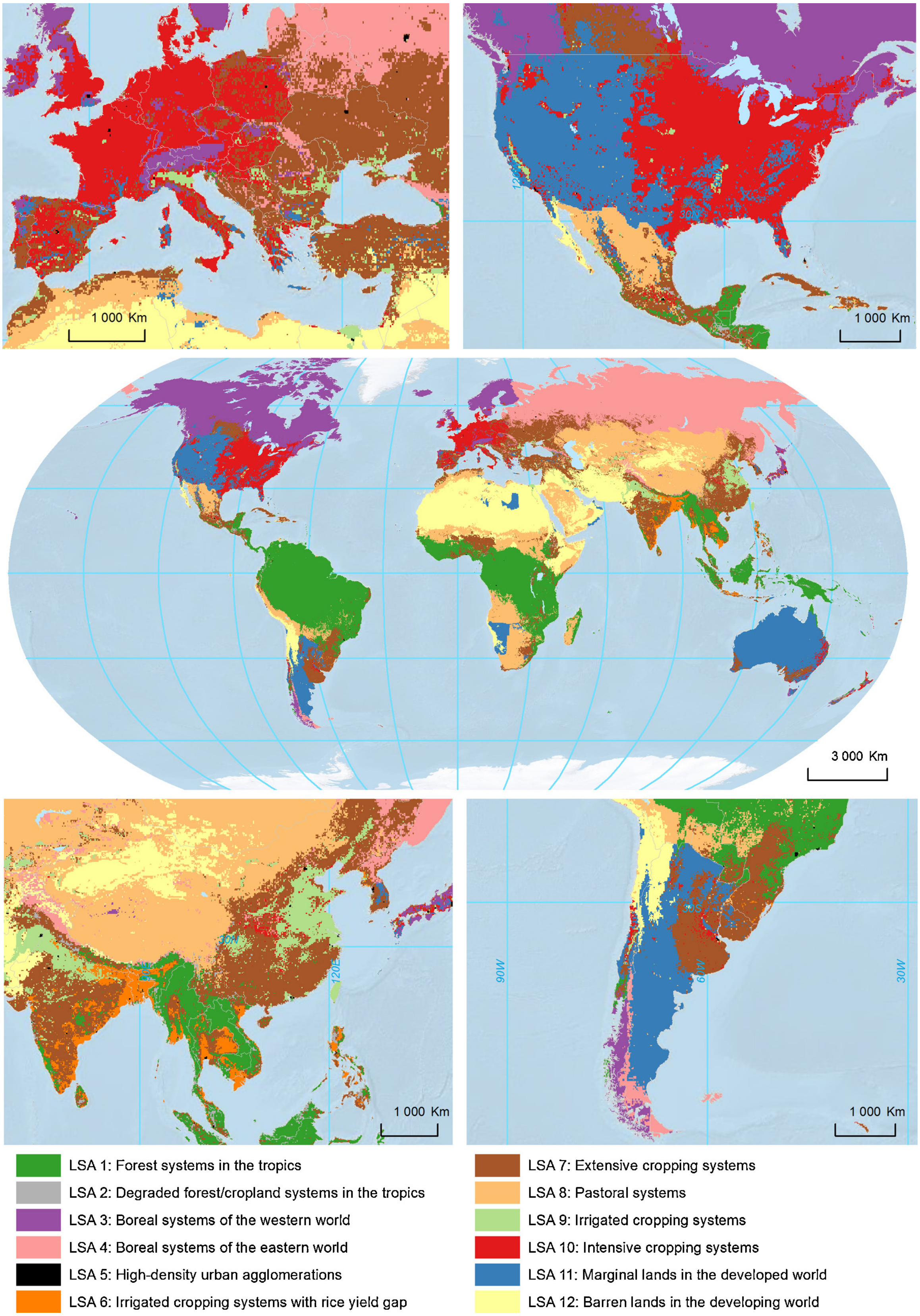

Fig. 1. Global land system archetypes: world map and regional areas. The data for this classification refer to the year 2005.

land productivity. Low and seasonally dependent NDVI corresponds to a cold and relatively dry climate that causes slow decomposition of organic material in soils and does not allow persistence of a large number of species. High GDP is a distinctive factor (average of 25,725 $ per capita) but less than 2% of GDP originates from the agricultural sector. Boreal systems are scarcely populated (average of 5 persons per km^2), far from cities and market places (average of 2270 min of travel time) but politically

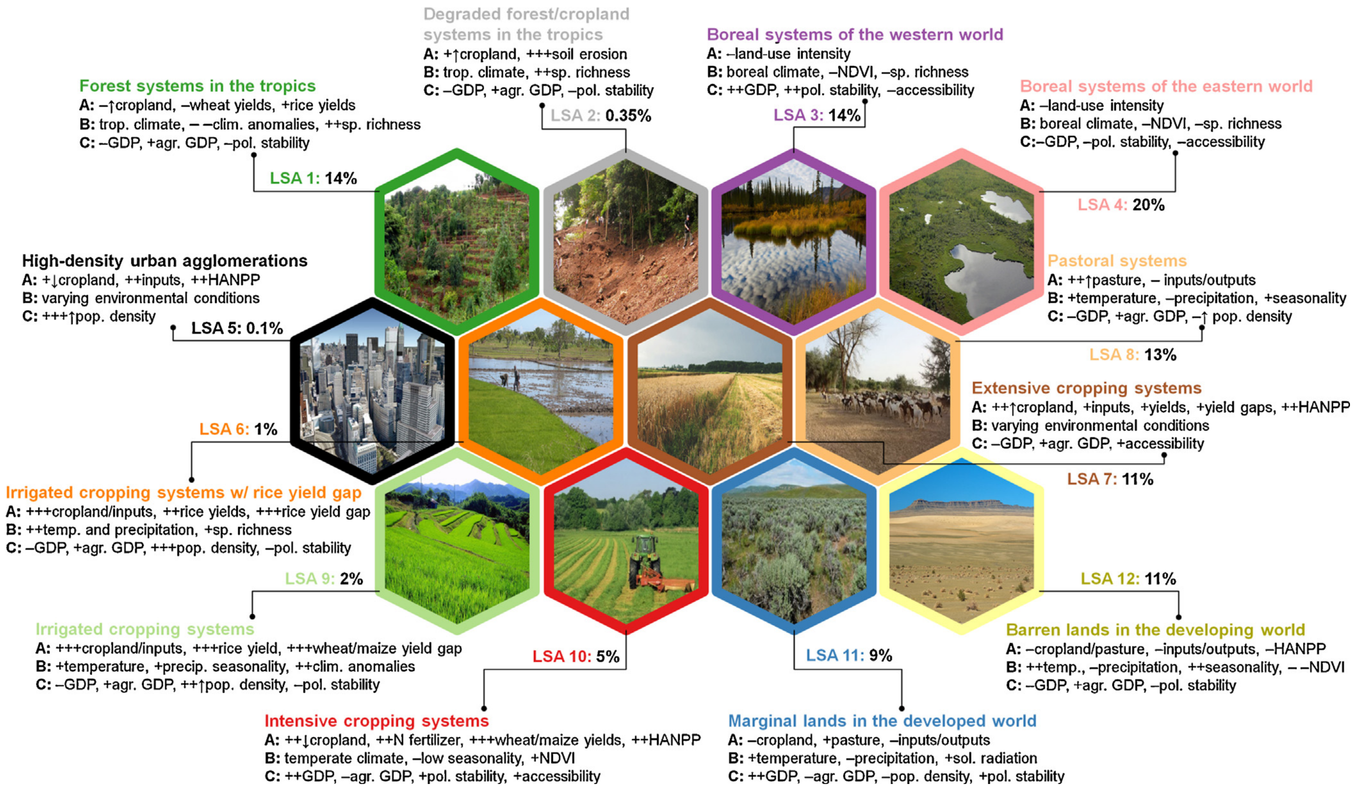

Fig. 2. Overview of land system archetypes (simplified version of Fig. A1 in the appendix), summarizing major land-use intensity indicators (A), environmental conditions (B) and socioeconomic factors (C) that best characterize each archetype. The + and – signs show whether the factor is above or below 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. The spatial position in this self-organizing map indicates similarity among land system indicators.

highly stable. This LSA occurs predominantly in Canada and Northern Europe but also in Patagonia and the higher elevations of Japan or the Alps.

Boreal systems of the eastern world (20% of terrestrial ecosystems) closely resemble the previous archetype with the exception of several socio-economic factors. While the climate and land-use intensities are almost the same, this archetype has on average substantially lower GDP (1779 $ per capita) but a higher share of GDP (6%) comes from the agricultural sector. The population density is comparable but the regions have slightly better accessibility to cities and market places (average of 1580 min) and have lower values of governance indicators. This archetype occurs predominantly in Russia and Northeast China.

High-density urban agglomerations (0.1% of terrestrial ecosystems) are characterized by extreme values of a few land system determinants, mainly population indicators (>15 s.d.). The population density is by orders of magnitude higher than in other archetypes (average of 7138 persons km^{-2}) and in the last 50 years it increased by 4319 persons per km^2. Urban agglomerations have an average cropland cover of 13% but its decrease in the last 50 years by 22 km^2 per grid cell indicates a rapid urbanization process on fertile land. High values for N fertilizers (23 kg ha^{-1}), irrigated areas (1035 ha per grid cell) and HANPP (51%) represent a legacy of formerly cultivated land but also reflects soil sealing and NPP losses from urbanization. As urban agglomerations are scattered throughout the world, most other factors are highly variable but the travel time to market places is naturally the lowest from all archetypes. Urban areas with lower population densities, which sum up to 0.5% of the terrestrial Earth surface (Seto et al., 2012) are part of other archetypes.

Irrigated cropping systems with rice yield gap (1% of the terrestrial ecosystems) are characterized by high cropland density (49%), large extents of irrigated areas (2613 ha per grid cell) and high inputs of N fertilizers (average of 33 kg ha^{-1}). Actual yields are low for wheat and maize and higher for rice (3 t ha^{-1} year^{-1}) but the yield gap for rice due to nutrient limitation is the largest from all archetypes. Climate factors point to relatively warm climate with high precipitation amounts and seasonality. While these regions have more than 17% of their GDP resulting from agriculture, they are economically very poor (GDP of 757 $ per capita) and politically unstable. The intense land-use pressure is illustrated also by dense population (509 persons per km^2) that increased by 307 persons per km^2 in the last 50 years. These areas have relatively good accessibility to cities and market places (average of 122 min) and occur predominantly in India, Bangladesh and Southeast Asia.

Extensive cropping systems (11% of terrestrial ecosystems) are characterized by high density of cropland (average cropland cover of 30%) and its high increase in the last 50 years (15 km^2 per grid cell). Although varying spatially, the extent of irrigated areas exceeds the global average and the land receives relatively high inputs of N fertilizer (approx. 13 kg ha^{-1}), while in the same time suffers from soil erosion (average of 9 Mg ha^{-1} year^{-1}). Yields of the three major cereals vary between 1 and 3 t ha^{-1} and almost 49% of NPP is appropriated for human use but there is still a substantial yield gap, especially for wheat and maize. The characteristic climate is mainly temperate but the conditions vary due to the wide spatial distribution of this LSA. GDP is below global average (4030 $ per capita) and about 12% originates from agriculture. The population density and its trend is highly variable but exceeds the global average (102 and 56 persons per km^2, respectively). Most regions are relatively well accessible, having a mean travel time of 208 min to cities and market places. This LSA occurs in Eastern Europe, India, China but also in South America and Sub-Saharan Africa.

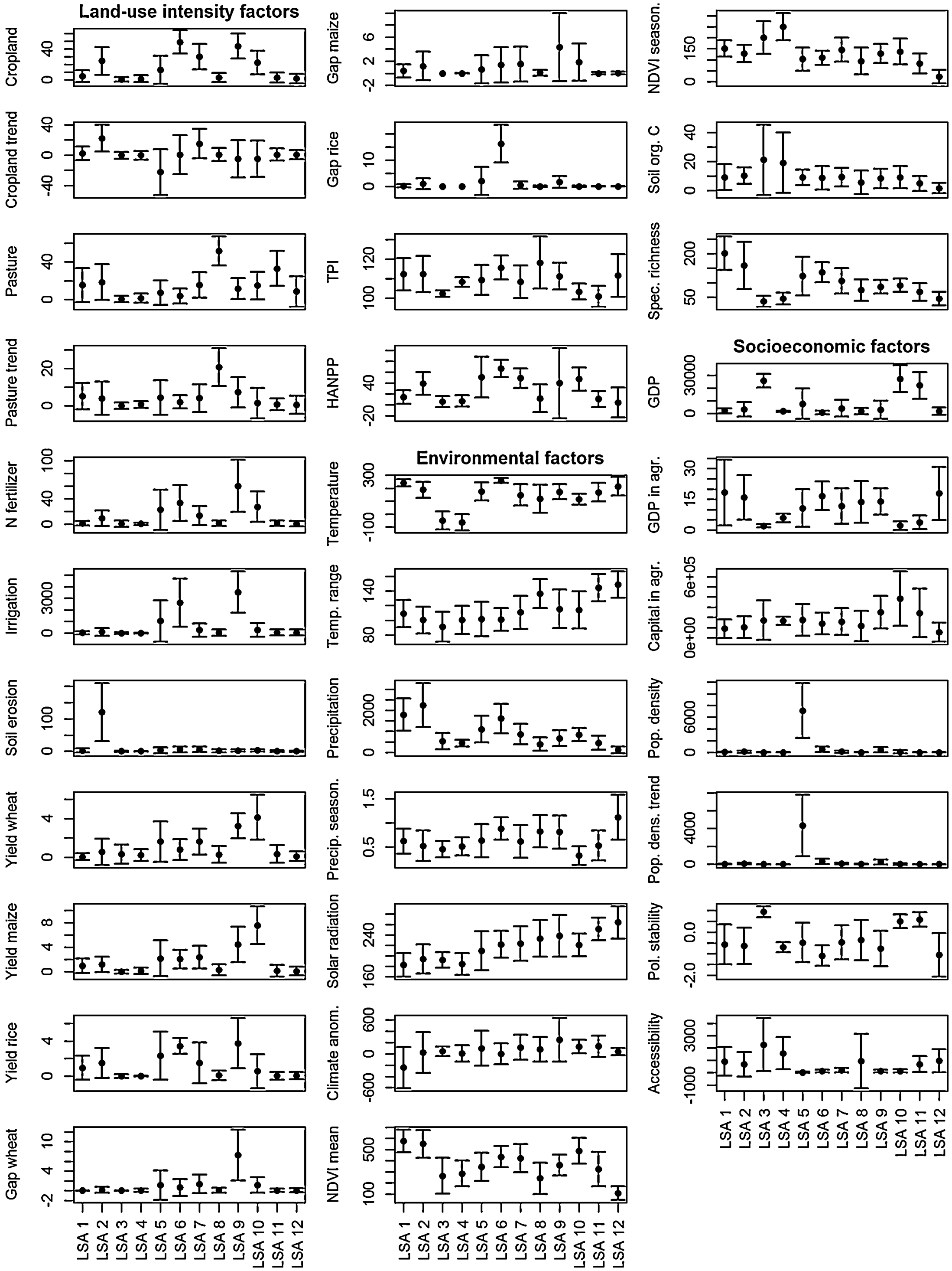

Fig. 3. Comparison of land-use input/output indicators, environmental conditions and socioeconomic factors that characterize each land system archetype. Dots represent mean values; whiskers represent standard deviations. For variable units, see Table 1.

Pastoral systems (13% of terrestrial ecosystems) are characterized especially by high densities of pastures and grasslands (average cover of 52%) and their increasing trends (average increase of 21 km^2 per grid cell). The agricultural inputs in the form of N fertilizer and irrigation are small, while the land has low actual and potential productivity. The total production index is relatively high in comparison to the base period but due to low cropland coverage, the total volume of cropland production is small. Low NDVI corresponds to drier climate but higher precipitation seasonality and diurnal temperature range. Countries that overlap with this LSA have relatively high proportion of GDP resulting from agriculture (14%), although the average total GDP is significantly lower than the global average (1772 $ per capita). These areas are scarcely populated (14 persons per km^2), although the population density has increased in the last 50 years (by 8 persons per km^2). Their accessibility is similar to the global average (945 min).

Pastoral systems occur predominantly in Central Asia but also in South and North Africa, Sahel, and in portions of Mexico and South America.

Irrigated cropping systems cover only about 2% of terrestrial ecosystems but represent managed landscapes with the highest agricultural inputs. This archetype is typical by having the largest extents of irrigated areas (3539 ha per grid cell) and extremely high inputs of N fertilizers (60 kg ha^{-1}). The cropland density is also one of the highest (average cover of 44%) but has decreased in the last 50 years by 5 km^2 per grid cell due to settlement encroachment. The yields are high for all three major cereals (3–5 t ha^{-1} year^{-1}) and about 39% of NPP is appropriated for human use but opportunities for agricultural intensification still exist, especially for wheat and maize. Considered climate factors point to relatively warm climate with high precipitation seasonality but the variation in climate anomalies suggests a potential threat for sustaining agricultural production. While these regions are politically unstable and economically poor (GDP of 2952 $ per capita), they have more than 14% of their GDP resulting from agriculture and relatively high capital investments in the agricultural sector. The intense land-use pressure is illustrated also by dense population (447 persons per km^2) that increased by 256 persons per km^2 in the last 50 years. Irrigated croplands have good accessibility to cities and market places (average of 116 min) and occur predominantly in India, China, Egypt, but also in Europe.

Intensive cropping systems (5% of terrestrial ecosystems) are characterized by a high density of cropland (cover of 22%) that has slightly decreased in the last 50 years and high inputs of N fertilizer (approx. 27 kg ha^{-1}). These inputs correspond to high yields for wheat and maize, although yield gaps for both crops still exist. The TPI has decreased in comparison to the base period but the total volume of production is higher than in other archetypes due to larger areas of harvested crops. Climate factors indicate a temperate climate with low seasonality that corresponds to productive ecosystems (high NDVI) but more than 47% of NPP is appropriated by humans. These regions are politically and economically stable (GDP of 27,287 $ per capita) and although only 2% of GDP originates from agriculture, they have the highest capital investments in the agricultural sector. Population density is on average 92 persons per km^2 and increased by 28 persons per km^2 in the last half century. Most regions are well accessible, having a short travel time (average of 134 min) to cities and market places. This LSA occurs mainly in Western Europe, Eastern USA and Western Australia.

Marginal lands in the developed world (9% of terrestrial ecosystems) are driven largely by pronounced positive socioeconomic factors and low values for indicators of land-use intensity. The average cover of pasture/grasslands is 33% but the average cropland cover is only 3% and has decreased in the last 50 years. Yields of major cereals are marginal but the conditions do not allow much potential to increase land-based production. The TPI even shows there has been a decrease in agricultural production in comparison to the base period. Temperature and precipitation indicators point to a warm and dry climate affected by frequent positive climate anomalies. These regions have similar values of socioeconomic indicators as the intensive cropping systems but the population density is only 6 people per km^2 with decreasing trend. This LSA occurs predominantly in Western USA, Australia, Argentina, but also in North and South Africa.

Barren lands in the developing world (11% of terrestrial ecosystems) consist of mostly barren and desert areas. Low densities of cropland (average cover of 2%) and pastures (average cover of 9%) allow only marginal agriculture with minimal yields and potentials for intensification. The limitation for growing crops is also emphasized by the low organic carbon content. Extremely low primary production as measured by NDVI corresponds to an extreme climate with high temperatures and their diurnal range, high solar radiation and low precipitation. The countries are economically poor (1954 $ per capita) but despite their low agricultural production and capital investments, about 18% of their GDP is generated by the agricultural sector. The population density in this archetype is only 12 people per km^2 but the settlement density varies substantially due to spatial clustering in urbanized areas. Regions in this archetype have the lowest political stability among all archetypes and include the Middle East, Saharan Africa and also deserts of Namibia, Gobi and Atacama.

4. Discussion

Identifying archetypical patterns of human–environment interactions presents a major challenge for land system science (Rounsevell et al., 2012; Turner et al., 2007). Simple approaches based on dominant land cover with limited consideration of land management are insufficient to draw a complete picture of coupled human–environment systems (Verburg et al., 2009). Integrated Assessment Models (IAMs; e.g. Bouwman et al., 2006; Schaldach et al., 2011) strive to capture interactions among biophysical and social systems but they represent land-use intensity in a simplified manner, e.g. by a single, aggregated factor of land management per world region. This represents a shortcoming for understanding the environmental impacts and socioeconomic costs of agricultural intensification. In this study, we offered an integrated view on land systems by directly accounting for the multiple dimensions of land use intensity in the context of prevailing environmental and socioeconomic conditions. Our classification identified interesting regional patterns that go beyond mono-causal analyses of a few land-use indicators. For example, the results revealed unexpected similarities in land systems across the globe (e.g. the extensive cropping archetype in East Europe, India, Argentina and China) but also showed a diversity of land systems at a sub-national scale, such as in China or India. Such findings challenge the view that land system drivers and outcomes can be modelled adequately at the national or macro-regional scales that are typical for IAMs (Bouwman et al., 2006).

4.1. Uncertainties in land system classification

As every classification scheme, LSAs represent a considerable oversimplification because land systems are inherently complex and dynamic. Still, our use of the SOM technique alleviated some of the subjective decisions needed in previous global classifications (e.g. Ellis et al., 2010; van Asselen and Verburg, 2012). Being an unsupervised data driven method, SOM allows clustering multidimensional data without the need of using expert rules or a priori classification thresholds. Moreover, SOM allows evaluating the quality of the classification procedure by calculating the distance of each grid cell in the multi-dimensional space to the mean values of the variables that best characterize the archetype. In our case, this quality assessment shows a homogeneous pattern of short distances for most locations, indicating good classification results (Fig. A2). Examples with higher distance values that require caution in interpretation are areas in the Nile Delta or in Western China. Here, some of the input variables have considerably higher or lower values than the mean values of the corresponding archetype (e.g. very large rice yield gap or poor accessibility, respectively) but are not different enough to be assigned to a different LSA. Larger distance values can be also found for many urbanized areas that do not have population densities high enough to be assigned to the LSA of high-density urban agglomerations.

While we used the best datasets on land use and environmental and social characteristics of land systems currently available, the main uncertainties in our classification stem from the quality and spatial resolution of input data. The quality of the global datasets used here was affected by (1) the techniques used to process remotely sensed data (e.g. for NDVI) or (2) the reliability of ground-based inventories (e.g. for socioeconomic data) collected by different monitoring and reporting methods (Fritz and See, 2008; Kuemmerle et al., 2013; Verburg et al., 2011b). Because remote sensing quantifies land use and environmental properties only indirectly, most variables were developed by the combination of remote sensing and inventory data, using three main approaches. First, climate or soil data were developed from point-based measurements using interpolation techniques. Second, land-use intensity data were developed by disaggregation techniques that combined statistical methods with satellite-based land-cover maps (e.g. for irrigation or yield data) or crop-type maps (e.g. for N fertilizer data) to transform national or subnational census data into grid-level metrics. Third, several datasets (e.g. soil erosion or yield gaps) linked direct remote sensing or ground-based measurements with outputs of mechanistic and simulation models. The nature of the data and applied models introduced different levels of uncertainty in the final classification. Consequently, many of the datasets were downscaled or upscaled from the original data or used directly in our classification at the national level (e.g. GDP or political stability).

Incorporating relevant land-use intensity, environmental and socioeconomic indicators is a crucial improvement in mapping global land systems, but many influential factors were still neglected due to the lack of data. For example, data on mechanization, farm size, crop rotation, grazing intensity or feed production are unavailable at the global scale, or they are associated with large uncertainties in specific regions (e.g. Africa). Data gaps are especially large for forestry, for which developing globally consistent information on the types of forestry systems (e.g. plantations, agroforestry) and harvest intensity is a major challenge (Kuemmerle et al., 2013). In addition, national and subnational policies such as agricultural subsidies or land access restrictions may drive the demand for different land functions. Similarly, cultural factors, ownership patterns or local economies can affect the decisions made by land managers (Lambin et al., 2001). Our assessment accounted for a wider range of determinants than previous land system models, but the influence of governance and culture is notoriously difficult to capture and is not available in adequate quality across broad geographic extents (Verburg et al., 2009).

Moreover, global datasets often capture information for different points in time. We used the year 2005 as a baseline because many datasets were not available in a full coverage for later years. This limitation, however, had an obvious effect on final results. For example, a part of Libya was included in the archetype marginal lands in the developed world because socioeconomic variables for 2005 describe it as a prosperous and politically stable country, although the situation has changed dramatically in the last several years. Improving existing land-use intensity metrics and incorporating new socioeconomic and institutional data is a key priority for land system science (Rounsevell et al., 2012). Developing time series of such data would also allow us to study archetypical patterns of land-use change and societal transitions.

4.2. Interpretation and application of land system archetypes

The land system archetypes we derived in this study can be used in a variety of ways to advance our understanding of global and regional human–environment interactions. First, classification of land systems at broader scales provides opportunities to detect generic patterns of major land pressures and environmental threats, and thus to identify regions that may require similar policy responses, or highlight heterogeneity (e.g. within countries), of which decision makers should be aware. For example, we show that severe loss of soil is most pronounced in three archetypes: degraded forest/cropland systems in the tropics, irrigated cropping systems with rice yield gap and extensive cropping systems (Fig. 3 and Table A2). Although soil erosion occurs in other systems too, these regions are particularly vulnerable to the loss of soil fertility because of their high agricultural inputs, low GDP and strong dependence on agricultural production. Similarly, water scarcity threatens land systems in which water availability is limited due to high irrigation (irrigated cropping systems) or low precipitation and seasonality (pastoral systems). While the opportunities to close yield gaps exist here through nutrient and irrigation management, sustainable adaptation of production to possible water scarcity is required. The analysis also shows a general pattern of pronounced climate anomalies for the forest systems in the tropics and irrigated cropping systems (although it cannot capture local impacts of climate change). Being rich in biodiversity, but economically and politically unstable with strong dependence on cropland production, these systems are particularly vulnerable to climate variability and further land transformation.

Second, land system archetypes can provide scientific evidence and action-oriented knowledge to cope with the challenges of global change. Studying land system archetypes can help us choose between alternative land-use strategies, e.g. expansion vs. intensification, to achieve production increases, and to assess the environmental and social outcomes of such choices. Foley et al. (2011) suggested that new approaches to agriculture (e.g. halting cropland expansion, closing yield gaps and increasing cropping efficiency) should be implemented to sustain future food demands while shrinking agriculture's environmental footprint. As these strategies cannot be used in a 'one-size-fits-all' manner, analyses of land systems can help identify strategies for particular regions and support the development of portfolios of solutions relevant for particular regions or countries (Seppelt et al., 2013). Several examples from our analysis highlight the relevance of such place-based approaches. For instance, our results suggest that, while the differences between realized and attainable yields are relatively small in intensive cropping systems, considerable opportunities for yield improvements exist in the LSAs of extensive cropping systems and irrigated cropping systems. These findings are supported by Mueller et al. (2012) who showed that Eastern Europe and Sub-Saharan Africa represent 'low-hanging' intensification opportunities for wheat and maize and Southeast Asia for rice. Here, large production gains could be achieved if yields were increased to only 50% of attainable yields. We also show that a large portion of LSAs is characterized by a considerably low political stability covering 48% of the terrestrial earth surface: forest cropping systems in the tropics, boreal cropping systems in the eastern world, both irrigated cropping systems and barren lands in the developing world. Any type of land management, no matter if focusing on preserving biodiversity, adaptation to climate change or closing yield gaps, needs to consider the limitations of land-use options due to social and political constraints. Some of these regions (e.g. irrigated cropping systems) also show high and increasing population density with main threats to water supply and low GDP.

Third, our archetypes allow for identifying areas and land systems that are underrepresented in terms of knowledge and data and therefore require further case studies to investigate land change in depth. Although remote sensing and global modelling have transformed the way we observe global land-use patterns, anthropogenic systems are not directly observable from space and cannot be modelled without a grasp of how humans interact with environment locally. The synthesis of land-use case studies at local scales is thus necessary but given the unstructured and multidisciplinary nature of place-based research, there is a need to better link and share its findings. Our archetypes can serve as an operational framework for such efforts and contribute to existing initiatives, e.g. GLOBE (http://globe.umbc.edu/), that help scientists identify gaps and opportunities for future research. However, our classification should be seen as an example of possible land system typologies that should be improved as new data and knowledge from regional studies become available. Such classifications based on finely-resolved data can be more complex or hierarchical for regions but will allow us investigating how global archetypes of land systems translate in specific regions and whether different factors characterize the patterns at finer scales.

Fourth, our archetypes can serve as a way to better represent land systems in global and sub-global assessments, and thus to better understand the impact of land-use change on biodiversity and ecosystem services, as well as the feedbacks of local and regional land change to the earth system (Verburg et al., 2011b). The concept provides a blueprint for spatially explicit global assessments focusing on various options and objectives in managing limited land resources. The methodological framework gives LSAs the potential to be used as entities in land change models and to spatially examine various scenarios of land system changes based on shifts in driving factors. Using LSAs as inputs in global models of land use dynamics can help us explore (i) the interactions and non-stationarity among multiple land-use drivers and (ii) the critical thresholds causing transitions of one land system to another. In addition, the concept can be applied to different sizes of SOM topologies and thus balance the trade-off between archetype generalization and data representation. This allows analysing land systems at different scales and testing whether responses to a particular policy change follow different paths in different land systems. Systematically linking biophysical and socioeconomic drivers to land-use trajectories is a prerequisite for the development and evaluation of sustainable land management strategies.

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Appendix A. Supplementary data

Supplementary data associated with this article can be found, in the online version, at doi:10.1016/j.gloenvcha.2013.09.004. These data include a Google KML file for a map of land system archetypes and the underlying land-use intensity, environmental and socioeconomic factors.

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Appendix 2

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LETTER

Investigating potential transferability of place-based research in land system science

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Abstract

Much of our knowledge about land use and ecosystem services in interrelated social-ecological systems is derived from place-based research. While local and regional case studies provide valuable insights, it is often unclear how relevant this research is beyond the study areas. 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. Here, we utilize the previously developed concept of land system archetypes to investigate potential transferability of research from twelve regional projects implemented in a large joint research framework that focus on issues of sustainable land management across four continents. For each project, we characterize its project archetype, i.e. the unique land system based on a synthesis of more than 30 datasets of land-use intensity, environmental conditions and socioeconomic indicators. We estimate the transferability potential of project research by calculating the statistical similarity of locations across the world to the project archetype, assuming higher transferability potentials in locations with similar land system characteristics. Results show that areas with high transferability potentials are typically clustered around project sites but for some case studies can be found in regions that are geographically distant, especially when values of considered variables are close to the global mean or where the project archetype is driven by large-scale environmental or socioeconomic conditions. Using specific examples from the local case studies, we highlight the merit of our approach and discuss the differences between local realities and information captured in global datasets. The proposed method provides a blueprint for large research programs to assess potential transferability of place-based studies to other geographical areas and to indicate possible gaps in research efforts.

1. Introduction

Understanding the interactions between people, land use and the environment is a central challenge for land system science (Rounsevell *et al* 2012). Much of our knowledge on land systems and the goods and services they provide is derived from place-based research and local assessments of ecosystem services (ESS). Place-based research of land use typically takes the form of case studies rooted in a particular place and context (van Vliet *et al* 2015). As a bottom-up approach, it is used to characterize the drivers and consequences of land use and its change in a specific location. Case studies have been used to estimate world's potentially available cropland (Lambin *et al* 2013), to reveal the complexity of coupled human and natural systems (Liu *et al* 2007), to assess the role of protected and managed forests for the long term maintenance of forest cover in the tropics (Porter-Bolland *et al* 2012), or to identify opportunities for enhancing the relevance of ESS assessments for decision making (Förster *et al* 2015).

The generalization and transferability of results from place-based research, however, is inherently limited because the drivers and processes of land use are complex, and their outcomes are contingent upon specific geographical context, including prevailing social, economic, political and cultural conditions. This limitation is especially true for land systems, i.e. social-ecological systems (SESs; Ostrom 2007), in which the interactions of different agents can be mediated through direct and indirect linkages and feedbacks with the physical environments (Letourneau *et al* 2012). Unlike studies with controlled research design, case studies collect empirical evidence on land-use phenomena in their real-world context and rely on non-random selection of sites whose unique characteristics facilitate meeting specific research goals. Consequently, the types and levels of land-use intensity, the environmental conditions, the social and political settings, and the spatio-temporal scales may vary substantially across sites (van Vliet *et al* 2015).

The outcome of place-based research is thus an evolving model that accounts for observed properties and behavior of the studied land system but also allows formulating hypotheses applicable to previously unstudied areas that have similar properties (Billick and Price 2010). Here we assume that similarity of land systems constitutes the potential for transferability, i.e. the more similar two sites are in terms of land use, environmental and socioeconomic conditions, the higher the probability that methods, results and conclusions from a project site prove applicable at a similar site. However, where these geographical sites with similar properties are located is typically unknown or not part of the research agenda. Therefore, given the variable design and multidisciplinary nature of place-based research, there is a need to better link the findings of the many case studies conducted and assess their relevance beyond the study areas.

Biomes, ecoregions and landscape typologies may provide a starting point for such efforts, but the applicability of biogeographical frameworks is limited because they do not incorporate human land use or reduce it to a single dimension of disturbance (Martin *et al* 2014). The use of integrative models of human-environment interactions has increased over the last years, after various global datasets on crop yields (Monfreda *et al* 2008), fertilizer use (Potter *et al* 2010) and other land-use intensity indicators became available (Kuemmerle *et al* 2013). For example, the anthrome framework was used to map the rate of landscape transformation over centuries (Ellis *et al* 2010) or to describe the current distribution of conservation efforts at the global scale (Martin *et al* 2014). New classifications of land systems were developed for their use in Integrated Assessment Models, in order to examine environmental consequences of interactions between economic, social and biophysical systems (Letourneau *et al* 2012, van Asselen and Verburg 2012). In addition, initiatives such as GLOBE (Ellis 2012; http://globe.umbc.edu) emerged to facilitate synthesis of case studies by providing an online database and tools for assessing the global relevance of land-use case studies based on their geographical context (Magliocca *et al* 2015).

Most recently, the concept of land system archetypes (LSAs) was developed in response to the calls for frameworks that incorporate multiple dimensions of land-use intensity in SESs (Václavík *et al* 2013). As agricultural intensification, including ecological intensification (Pywell *et al* 2015), is likely to continue in the future, it is becoming clear that a wider spectrum of land-use intensity metrics needs to be considered (Erb *et al* 2013, Kehoe *et al* 2015). LSAs utilize a wide range of such metrics and offer an alternative view on land systems by integrating various measures of land-use intensity in the context of prevailing environmental and socioeconomic conditions. The framework is well suited to increase the global relevance of place-based research because it provides a first step for classifying land systems with similar properties as those represented in the investigation sites.

Here, we adapt the existing framework of LSAs (Václavík *et al* 2013) and propose a new approach to examine potential transferability of place-based research. We apply our approach to twelve regional projects of the German Sustainable Land Management (SLM) Program, a large-scale funding initiative that provides a platform for research of sustainable land-use across four continents, with the focus on deriving sustainability transformation strategies. For each case study, we define the 'project archetype', i.e. the unique land system present in the study area, based on a synthesis of global land system indicators. Assuming that similarity in land-use intensity and environmental and socioeconomic conditions among regions is a basic pre-condition for transferability, we address the following questions: (1) Where are the areas to which the research methods, results and conclusions of local case studies from the SLM Program can be potentially transferred? (2) Are there regions across the world that are under- or over-represented by the research within the SLM Program? Using specific examples from selected regional projects, we highlight the merit and applicability of our approach, describe the differences between local realities and information captured in global datasets, and discuss the optimal strategies for improving transferability in the future. We also discuss the criteria that determine and limit transferability of place-based research, thus testing our hypothesis that similarities constitute transferability potentials.

2. Materials and methods

2.1. Case studies

We analyzed twelve case studies that are part of the SLM Program, funded by the German Federal Ministry for Education and Research (Eppink *et al* 2012). Their objective is to improve the understanding of interacting ecological and socioeconomic systems, and to foster transformations towards more SLM (see table 1 for an overview of project focus, research questions and adopted measures). The projects have similarities in common drivers of change, such as population growth, developments in economic markets and climate change. There is also a distinct overlap in the ecosystem services considered, such as food production, fresh water supply and climate regulation. The projects are conducted in 13 countries across four continents with a wide range of conditions that define the underlying LSAs (figure 1). The spatial scale of the projects ranges from a few hundreds to several hundred thousands of square kilometers.

2.2. Data

We considered the same set of 32 indicators of land-use intensity, environmental conditions and socio-economic situation as previously used to define global LSAs (see table A1 in the supplementary material). Details on the datasets and the indicator selection are provided in Václavík *et al* (2013). In summary, we compiled 15 land use datasets that measure different aspects of agricultural intensity in terms of inputs, outputs and system metrics (sensu Kuemmerle *et al* 2013). For input metrics, we chose maps of cropland and pasture cover (Klein Goldewijk *et al* 2011) and also calculated their changes over the last 50 years to account for temporal trends. In addition, we considered the extent of areas equipped for irrigation (Siebert *et al* 2007) and the levels of nitrogen (N) fertilizer input (Potter *et al* 2010). For output metrics, we included crop yields for wheat, maize and rice (Monfreda *et al* 2008), because these crops represent approximately 85% of global cereal production (Hafner 2003) and are grown in most of the considered regional projects. For system-level metrics, we selected yield gaps for wheat, maize and rice (IIASA/FAO 2012), the human appropriation of net primary production (HANPP; Haberl *et al* 2007), and soil erosion caused by water and tillage (Van Oost *et al* 2007).

To represent environmental conditions, we used five uncorrelated bioclimatic variables from the CliMond database (Kriticos *et al* 2012) accompanied by climate anomalies interpolated from NOAA's long-term measurements of land surface temperatures (Menne *et al* 2009). For biophysical factors that reflect productivity and growth conditions of ecosystems, we included datasets on normalized difference vegetation index (NDVI) (Tucker *et al* 2005) and soil organic carbon (Batjes 2006). Vertebrate species richness for mammals, birds, reptiles and amphibians were derived from expert-based range maps (BirdLife International 2012, IUCN 2012) as a biodiversity indicator reflecting both natural conditions and long-term effects of land management (Green *et al* 2005, Phalan *et al* 2014). For economic indicators of land systems, we used three indices provided by the Food and Agriculture Organization (FAO) at a national level: gross domestic product (GDP), the proportion of GDP resulting from agriculture and the capital stock in agriculture. As socioeconomic factors and indicators of human pressure on land, we used gridded data on population density (CIESIN 2005), the world governance index of political stability (Kaufmann *et al* 2010) and the global map of accessibility that measures travel time to major cities and market places (Uchida and Nelson 2009). We are aware that the geographical scope of the different parameters is not identical, and that taking data aggregated at national or regional scale can mask significant deviations in the research sites; one example is discussed below.

The requirement was that these datasets are available for the entire terrestrial surface of the world, so that transferability potentials can be investigated beyond the study areas of our case studies. The land-use data were derived for circa the year 2005, the time period where such datasets are richest at the global scale. Prior to the final variable selection, we inspected Pearson correlations between all variables in order to avoid redundancy in the input information (see table A2 in the supplementary material). Our final set of input indicators included only those with $|r| < 0.7$ (Dormann *et al* 2013). All data were aggregated to the

Table 1. Regional projects within the German Sustainable Land Management Program focus on various aspects of land use and ecosystem services across four continents. Documents and videos summarizing each case study can be accessed at the program's website (http://modul-a.nachhaltiges-landmanagement.de/en/projects/).

Project/area	Focus	Research question	Measures
Carbiocial: 119 170 km^2	Carbon sequestration, biodiversity and social structures in Southern Amazonia: models and implementation of carbon-optimized land management strategies	Optimize land management to minimize negative feedback by land use change in the frame of climate change and socio-economic development	Decision support systems for carbon-optimized land use by region-specific modeling of land use impact
CC-LandStraD: 357 021 km^2 Analyzed focus area: 6310 km^2	Interdependencies between land use and climate change: strategies for a sustainable land management in Germany	How can be a sustainable land use in 2030 in Germany? How to model the interactions between land use and climate change in Germany?	Strategies for sustainable land management and its contribution to climate change mitigation in Germany
COMTESS: 600 km^2	Sustainable coastal land management: trade-offs in ecosystem services	Which strategies can promote a sustainable management of vulnerable coastal landscapes?	Adapted water management strategies including a sustainable agricultural land use under changing hydrological conditions
INNOVATE: 377 000 km^2	Interplay among multiple uses of water reservoirs via innovative coupling of substance cycles in aquatic and terrestrial ecosystems	Which governance options promote sustainable ecosystem services and economic viability under climate change conditions?	Decision support systems based on constellation analysis for land and water use based on modeled land and water use scenarios
KULUNDA: 93 230 km^2	How to prevent the next global dust bowl? Ecological and economic strategies for sustainable land management in the Russian steppes: a potential solution to climate change	How degradation and desertification processes can be mitigated by development and implementation of adequate sustainable land management practises?	Adopted agricultural management and tillage operation for advanced steppe restoration
LEGATO: 1575 km^2	Land-use intensity and ecological engineering: Assessment tools for risks and opportunities in irrigated rice based production systems	How to advance long-term sustainable development of intensive land use systems, against risks arising from multiple aspects of global change, by quantifying the dependence of ecosystem functions (ESF) and the services (ESS) they generate in agricultural systems in South East Asia?	Implementation of ecological engineering, organic farming for landscape scale management and sustainable intensification
LUCCi:12 350 km^2	Land use and climate change interactions in the Vu Gia Thu Bon river basin, Central Vietnam	Which role does land use play for GHG emissions? Which strategies for sustainable land and water management can cope with climate change impacts?	Implementation of land-use planning and water management strategies for mitigation of GHG emissions in agriculture and forests based on regional climate change scenarios by bio-economic optimization model
SASCHA: 1200 km^2	Sustainable land management and adaptation strategies to climate change for the Western Siberian grain belt	How to mitigate the negative impacts of agricultural land-use change on ecosystem services and biodiversity in Western Siberia?	Modeled future land-use scenarios; toolkits for monitoring change and land-use planning; written guidance and training for policymakers
SuLaMa:7500 km^2	Participatory research to support sustainable land management on the Mahafaly plateau in south-western Madagascar	How to reconcile biodiversity conservation and the maintenance and enhancement of ecosystem services with economic land management?	Participatory determination of strategies for implementing a jointly developed sustainable land management plan
SuMaRiO: 650 000 km^2	Sustainable management of river oases along the Tarim River, China	How to support oasis management along the Tarim River (TR) under conditions of climatic and societal change?	Enhanced water management and land management particularly with regard to ecology on basis of scientific

Table 1. (Continued.)

Project/area	Focus	Research question	Measures
			results and their application in a decision support system tool
SURUMER: 265 km^2	Sustainable Rubber Cultivation in the Mekong Region—Development of an integrative land-use concept in Yunnan Province, China	How does the current practice of rubber management affect Ecosystem Functions and Services (ESF/ESS)? And how can the system be improved towards sustainability?	Development and dissemination of improved rubber management schemes, stakeholder involvement, diversification of production
The Future Okavango:430 000 km^2	Scientific support for sustainable land and resource management in the Okavango Basin	How to improve land use and resource management with scientific knowledge?	Development of tools (scenarios, storylines, DSS) and strategies for sustainable land use and river basin management

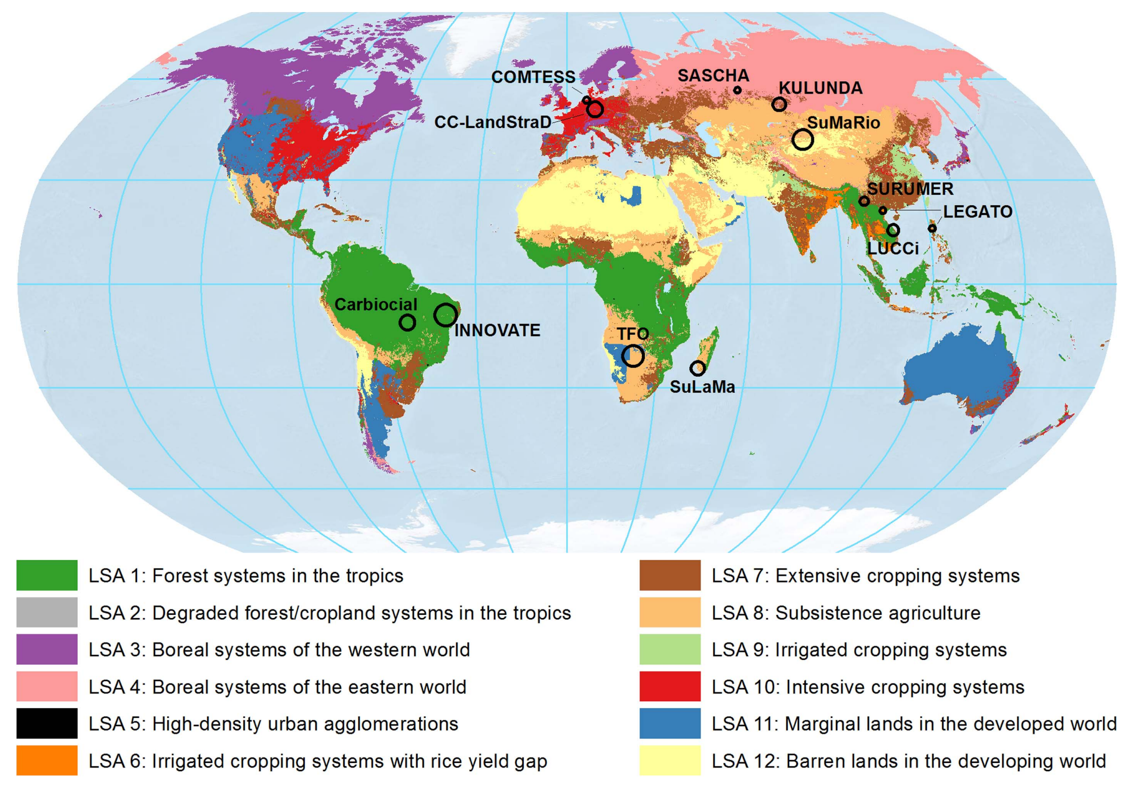

Figure 1. Geographical locations of investigated regional projects and their distribution in global land system archetypes defined by Václavík *et al* (2013) based on clustering of similar land-use intensity, environmental and socioeconomic conditions. The size of the project symbol is relative to the project's study area. The geographic locations of project study areas were obtained from the Geoportal of the SLM Program at: http://geoportal-glues.ufz.de/.

spatial resolution of 5 arc-min (~9.3 × 9.3 km at the equator).

2.3. Analysis of transferability potentials

We estimated transferability potentials for the twelve regional projects by calculating the statistical similarity of all 5 arc-min pixels across the world to the unique land system present in each project study area. We assumed that if the project study area overlaps with a specific LSA (Václavík *et al* 2013), then its research is potentially relevant for other geographical regions that belong to the same archetype. However, the original global classification, based on a self-organizing map clustering of the same variables as used here, is relatively coarse and thus high variability in land-use intensity and other conditions exists within the individual archetypes (Václavík *et al* 2013). Also, the availability, resolution

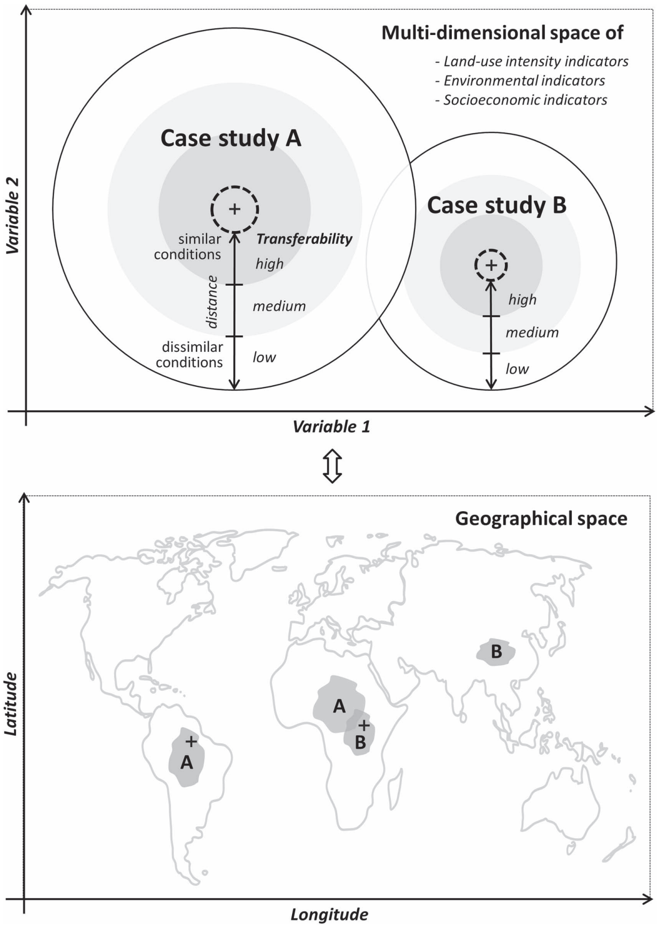

Figure 2. Conceptual diagram of identifying and mapping potential transferability of place-based research. The upper rectangle represents a multidimensional space defined by land-use intensity, environmental and socio-economic indicators. The crosses denote the 'project archetypes', i.e. the mean conditions in the study areas of two hypothetical case studies; the circles denote the range of conditions present in the case study areas, with 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 the project archetypes may differ in size or overlap both in the multi-dimensional and geographical space.

and quality of underlying data vary across the world, suggesting that the precision of an archetype definition is not always comparable across regions. Therefore, we extended the original archetype framework and adopted a three-step approach to quantify the degree of similarity between given case studies and other regions around the world (figure 2).

First, we analyzed the conditions in each project as reflected by the considered variables and determined the 'project archetype', i.e. the unique land system in the study area. Prior to the analysis, we checked the data for skewed distributions and removed extreme outliers. Because of their differing units, we normalized all variables to zero mean and unit variance, so the results can be interpreted in terms of how much and in which direction the project conditions deviates from the global average. We defined the *project archetype* as the combination of the means A_i for all variables $i = 1,\ldots, 32$ calculated as:

$$A_i = \frac{1}{p}\sum_{n=1}^{p} x_n \qquad (1)$$

with x being the normalized value of each variable and p being the total number of cells in the regional project. Second, we calculated statistical similarity of the project archetype (represented by each grid cell within the project) to each global grid cell in the multi-dimensional space defined by considered variables, assuming higher transferability potentials in locations with similar land systems (figure 2). As a measure of similarity, we used an absolute distance D, calculated as:

$$D = \frac{1}{g \times p \times v}\sum_{i=1}^{v}\sum_{n=1}^{p}\sum_{m=1}^{g} |x_{i,n} - x_{i,m}| \qquad (2)$$

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 project and v being the number of considered variables. Third, using the inverse of distance D, we mapped the gradient of transferability

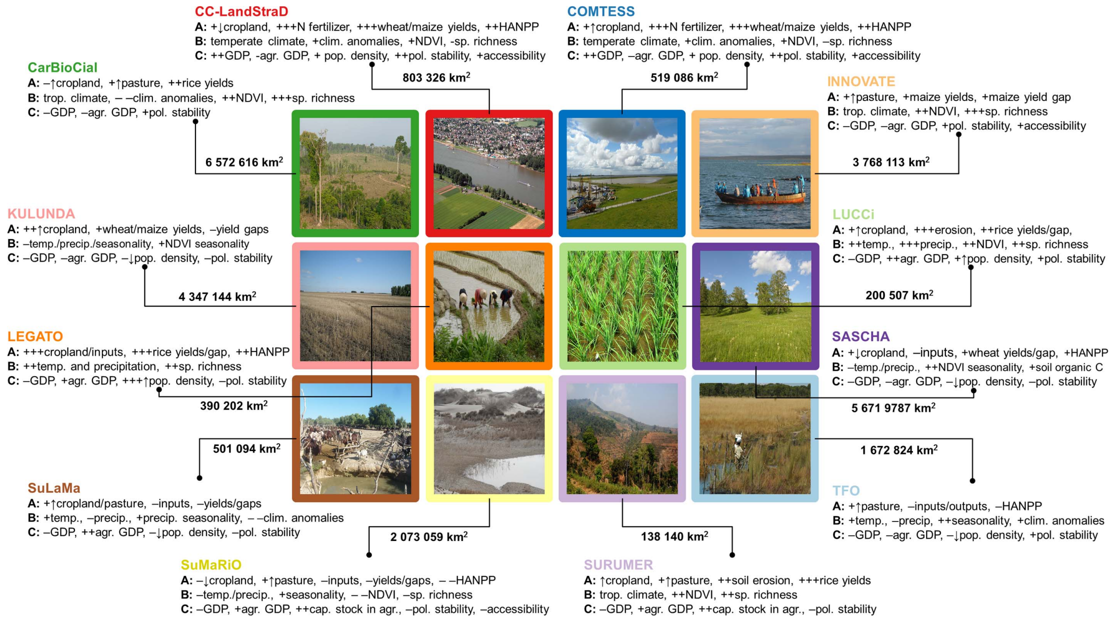

Figure 3. Project archetypes of the Sustainable Land Management Program. Summarized description of (A) land-use intensity indicators, (B) environmental conditions, (C) socioeconomic factors that characterize each project. The + and − signs show whether the factor is above or below global average (+ is 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 in km^2 show the total areas of regions identified as having a high level of transferability potential (the top 25% of the gradient).

potentials for each project in the geographical space (figure 2). For better visualization, we divided the gradient of transferability potentials into four equal classes, with the lowest 25% distance interval representing 'high' transferability potential and the highest 25% distance interval representing 'no' transferability potential.

We assumed that the variability in underlying conditions, which is likely to be higher for projects with larger study areas, may affect the total area estimated as having high transferability potential. Therefore, we used ordinary least square (OLS) regression analysis to examine the relationship between the total variability of conditions in the study area (calculated as the sum of standard deviations for all variables) and the extent of the 'high' transferability level. All analyzes were conducted in R version 3.2.0 (R Development Core Team 2011), using the libraries 'rgdal' (Keitt *et al* 2011) and 'vegan' (Oksanen *et al* 2013).

Finally, we chose one project, SASCHA (table 1, figure 1), for which we refined the analysis of transferability potentials with finer-scale data from its study area in Western Siberia. To illustrate the potential effects that differences in global versus local data may have on the final analysis, we replaced the values of six original variables (from datasets with a global extent) with those for the same variables from local datasets. Local datasets of cropland area (ha), pasture area (ha), N fertilizer use in agriculture (kg ha^{-1}), wheat yield (t ha^{-1}) and human population density were obtained from the Territorial Authority of the Federal State Statistics Service of the Tyumen Region (TyumStat 2015a, 2015b). The data were available at a district-level resolution for the entire province of Tyumen (160 000 km^2), which has 22 districts with variable climate, socio-economic conditions, suitability for agriculture, cropland and pasture extent and land-use trends (Kühling *et al* 2016). The global GDP estimate for Russia was replaced by an official local estimate (the 'regional domestic product') for the Tyumen province (RosStat 2015).

3. Results

Each case study was characterized by a unique project archetype defined by a specific combination of land-use intensity, environmental and socioeconomic conditions (figure 3). The results identifying a gradient of transferability potentials for each of the twelve case studies are shown in figure 4. The mapped levels of transferability potentials varied regionally, often exhibiting spatial clustering of highly similar conditions around the project sites (e.g. for CC-LandStraD, COMTESS, LEGATO). In contrast, highly similar conditions were found for a number of projects in locations that are geographically distant from the study sites (e.g. for CarBioCial, KULUNDA, SASCHA). This corresponds with the original archetype classification which identified relatively large areas of similar land systems across the tropics and the boreal biome.

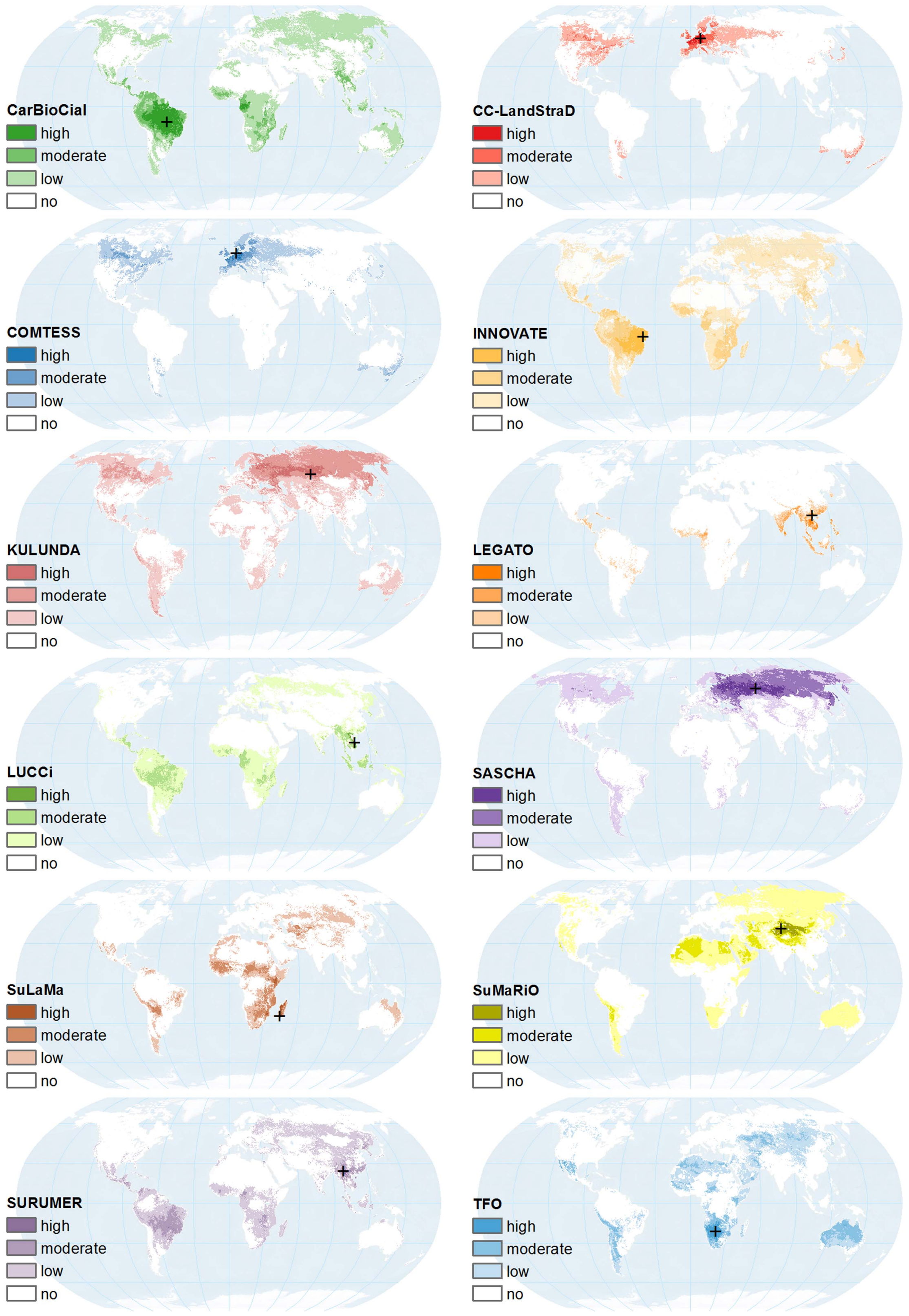

Figure 4. Mapped transferability potentials for the 12 regional projects based on all 32 variables. Areas with conditions similar to those in the regional projects are assumed to have higher transferability potentials. The gradient of transferability potentials is divided in four equal classes, ranging from high to no transferability potentials. For all RPs the same threshold is used, so the levels of transferability potentials and their spatial extents are comparable among the projects. The black cross in each map denotes the location (centroid) of each project's study area.

The top 25% of the calculated transferability potentials (the 'high' level in figure 4) contained areas with extents ranging from 138 140 km^2 to 6572 616 km^2 for SURUMER and CarBioCial, respectively (figure 3). A spatial overlay of these areas with high transferability potentials (top 25%) highlighted

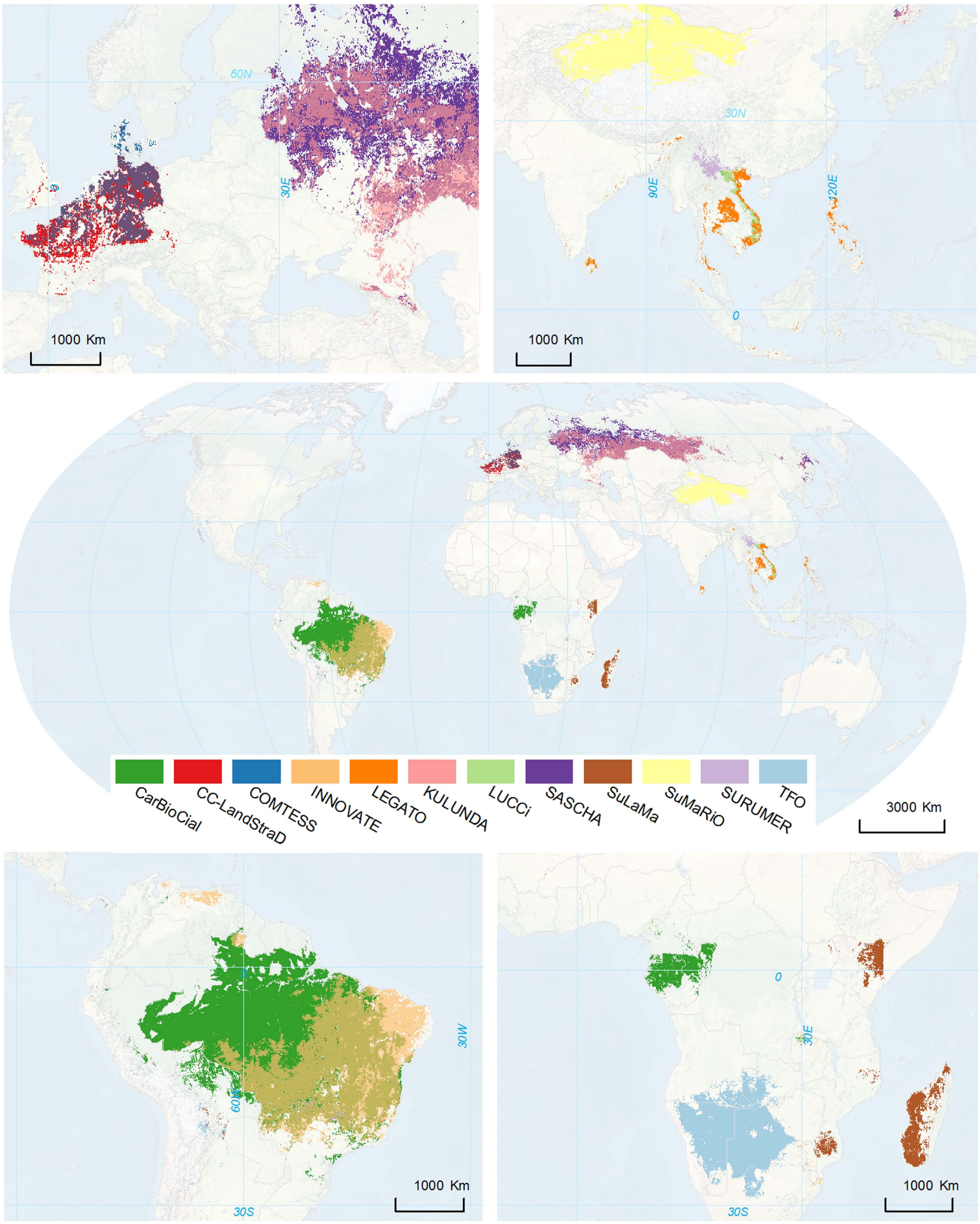

Figure 5. Areas with high transferability potential (top 25% of the transferability gradient), highlighting regions for which the research of the SLM Program is most relevant. The areas with no color, e.g. in North America, Central Africa and the Middle East, are under-represented in the Program's research efforts. In contrast, several regions are simultaneously covered by multiple projects. In the upper left inset, there is a large spatial overlap between CCLandStraD and COMTESS in central Europe (with COMTESS extending more to the coastal areas in the north), and between SASCHA and KULUNDA in Asia. In the lower left inset, there is an overlap in transferability potentials for CarBioCial and INNOVATE.

the parts of the world, for which the research of the SLM Program is most relevant (figure 5), but it also revealed areas that are likely under-represented by the SLM Program, e.g. in North America, Central Africa and the Middle East. In contrast, several regions were predicted as having high transferability potentials for more than one project. For example, large spatial overlaps of high transferability potentials exist for CC-LandStraD and COMTESS in Western Europe, for SASCHA and KULUNDA in Western Siberia and for CarBioCial and INNOVATE in central South America.

The differences and overlaps in project transferability potentials were also apparent when inspecting the combination of variable values that characterize each regional project (figure 6). For example, CC-LandStraD and COMTESS had similar values for most variables but differed slightly in cropland area and

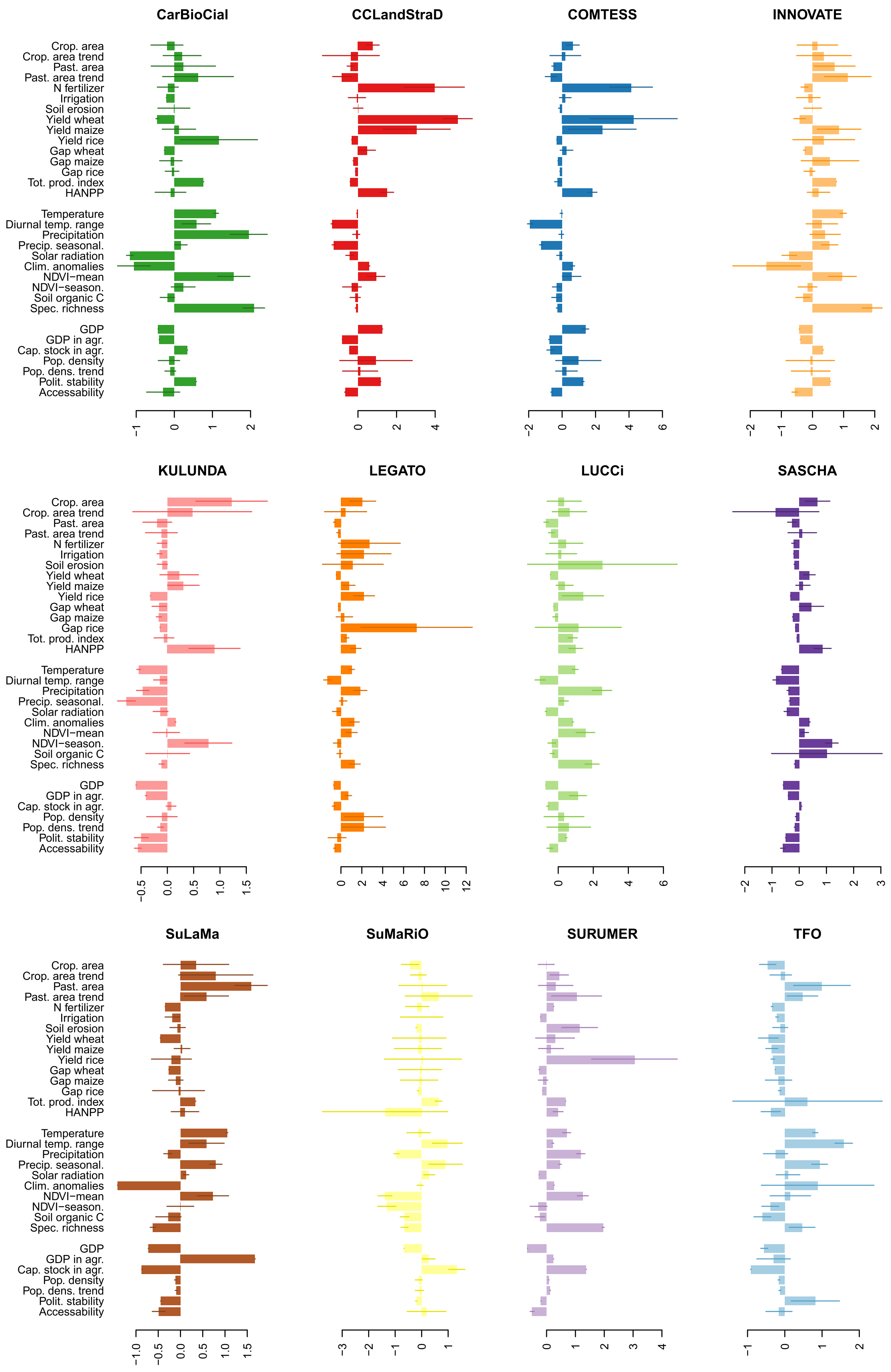

Figure 6. Detailed characterization of land systems in regional projects, showing the combination of normalized variable values. Zero on the *x*-axis is the global mean, so the graphs show whether and how much an indicator is above or below the global mean. The bars represent mean values of the conditions in each study area; the whiskers represent standard deviation (variability of the indicator) within the study area.

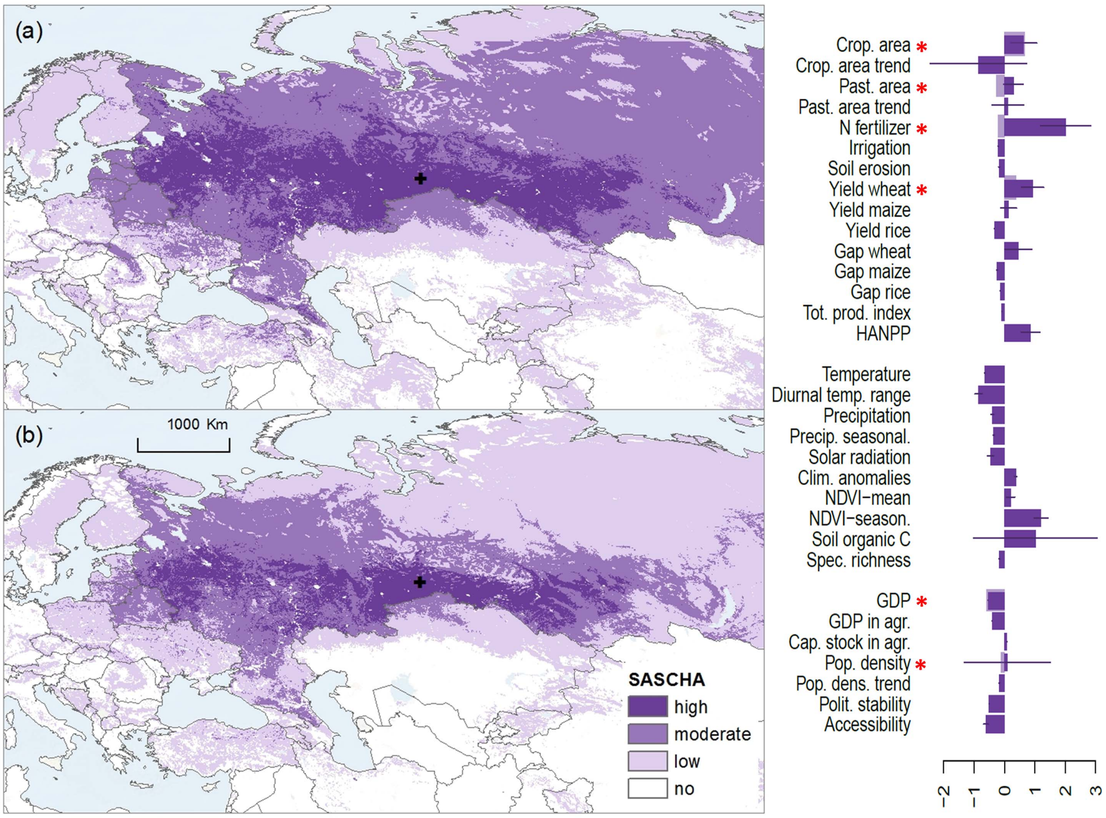

Figure 7. Transferability potential for the SASCHA regional project based on (a) global variables only and (b) refined with finer-scale datasets from the region. The chart on the right shows the combination of normalized variable values in the study area captured by the considered datasets. Variables for which local data were available are marked with red asterisks; their original values captured by the global datasets are displayed as light purple bars for comparison. The black cross in the maps denotes the project location.

yields (see also figure A1 for non-standardized values in the original units). While several projects fell into the same global LSA (figure 1) defined by Václavík *et al* (2013), their project archetypes may still differ largely, suggesting a high regional diversity of conditions in the globally defined land systems. Even the conditions within the project study areas varied substantially for some case studies (figures 6 and A1). However, no significant relationship was found between the total variability of conditions in the study area and the extent of the 'high' transferability potential (OLS, $R^2 = 0.163, p = 0.194$).

The refined analysis for SASCHA revealed similar patterns of transferability potentials across the Western Siberian grain belt compared to the analysis based on values of global datasets. However, the area estimated to have a 'high' transferability potential decreased to about 48% (2742 136 km^2) of the area identified in the original analysis (figure 7). The global estimates of cropland area proportion closely matched the local statistics from the region (approx. 16% of cropland cover in both global and local datasets). However, the global values for realized wheat yield, GDP and population density were slightly lower than those collected from local sources. Larger differences between global and local data occurred for pasture area (difference of 12%) and N fertilizer (difference of 31 kg ha^{-1}).

4. Discussion

Our results show that there are areas beyond the projects' study sites that have similar land systems as those identified in the twelve regional projects of the SLM Program. While the degree of mapped transferability potentials was highly variable in different parts of the world, it was typically clustered around the project sites (figure 4). This pattern suggests that considered land-use intensity, environmental and socioeconomic conditions are spatially dependent (i.e. autocorrelated) and that calculated statistical distance partially corresponds to geographical distance. On the other hand, high transferability potentials for some case studies were found in regions that are relatively far from the project sites. This was typical for projects where variable values were close to the global mean or where the project archetype was driven by large-scale environmental or socioeconomic conditions. For example, areas with high transferability potentials for KULUNDA and SASCHA were identified across the entire Eurasian steppe belt. This is likely due to the similar biophysical conditions (climate, soils) along the latitudinal ecozones of Eurasia (Degefie *et al* 2014, Kamp *et al* 2015). Similarly, the socioeconomic conditions are rather comparable across Russia due to a strongly centralized political and economic system.

The spatial overlay of the high transferability potentials for all projects (figure 5) highlighted not only regions for which research of the SLM Program is most relevant but revealed also 'white spots' that constitute archetypes of low transferability potentials due to relatively large differences among the projects in the underlying land system conditions. This shows that even when a project falls within a certain LSA, its transferability potential does not necessarily extend across the entire range of this land system because the globally defined LSAs still host a high diversity of conditions. This also confirms our assumption that the original archetype framework needed to be refined to allow a reasonable analysis of transferability potentials of regional case studies. However, we did not confirm our assumption that the level of variability in considered conditions within the project's study area affects the total area estimated as high transferability potential. The non-significant relationship between the two factors can be caused by the complexity of considered land system indicators, the spatial distribution of their values across the world, the selection of the threshold used to define the 'high' transferability potential level (i.e. the top 25% of the distance gradient), but also by the relatively small sample size ($n = 12$).

In contrast, we found several regions with spatial overlap of high transferability areas for multiple projects. The similarity in project archetypes of these case studies can be in large part attributed to the close proximity of their study sites. For example, the relative closeness of CC-LandStraD and COMTESS, both with study sites in northern and western Germany, resulted in 62% overlap of their areas with high transferability potential. Nevertheless, even at this scale and based on global datasets of land system indicators, our analysis was able to detect relatively small local differences between the project characteristics. CC-LandStraD that has the aim to analyze contributions of land management in Germany to climate mitigation has its study sites chosen to represent land systems of a developed high-tech country in a temperate climate zone and reliable political structures (Fick *et al* 2014). Indeed, this is reflected in the results that identified areas with high potential for transferability in large parts of Western Europe, especially Germany and France but also parts of Central Europe. In contrast, COMTESS that focuses on developing land use strategies to promote sustainable management of vulnerable coastal landscapes (Karrasch *et al* 2014) has its high transferability potentials situated more to the north. In addition to covering large portions of Germany and France, the estimated areas with high transferability potential extend to coastal areas of Belgium, the Netherlands and Denmark.

The refined analysis of transferability potentials for SASCHA revealed a dependency of the results on the resolution and accuracy of the considered input data (figure 7). Surprisingly, the global datasets captured the regional realities (represented by data from regional statistics) considerably well, although the indicators of pasture areas and N fertilizer were underestimated in the global datasets. This led to an overall decrease of the estimated transferability potentials in the refined analysis (e.g. lower transferability potentials in Ukraine due to differences in yields and socioeconomic conditions), but the general pattern remained largely similar, covering most of the Western Siberian grain belt (Kühling *et al* 2016). Similarly for SURUMER, which focuses on sustainable rubber cultivation in the Mekong Region, only few out of the 32 global variables had values that did not closely match the local reality (Hauser *et al* 2015). Of the land-use intensity indicators, both cropland area and the use of N fertilizer were underestimated. Recent data published by Xu *et al* (2014) point towards a total share of 22% of rubber, paddy rice and upland maize cultivation in the SURUMER wider research area, as opposed to about 10% of cropland area indicated in the global dataset. Also, the maize yields appear to be underestimated considering the availability of industrial fertilizer and presence of an agricultural extension system in China (Hu *et al* 2009). The FAO data for China (FAOSTAT 2010) indicate maize yields of 5.2 t $\mathrm{ha^{-1}}$, as opposed to less than 2 t $\mathrm{ha^{-1}}$ given by the global dataset. Soil organic carbon content may be also underestimated as the vast majority of rubber plantations are situated on soils cleared recently from forest (Hauser *et al* 2015).

We used a comprehensive set of global land system metrics with the highest resolution currently available. However, despite considerable improvements in global-scale geospatial datasets (Verburg *et al* 2011), the main sources of uncertainty remain in the quality of input data and the availability of socio-cultural information in a globally standardized format. The quality of datasets is affected by many factors, such as the reliability of ground-based inventories, processing techniques of remotely sensed records, positional accuracy, spatial scale of data aggregation or the difficulties in quantification and standardization (Kuemmerle *et al* 2013). Some land use indicators (e.g. yield gaps, N fertilization)

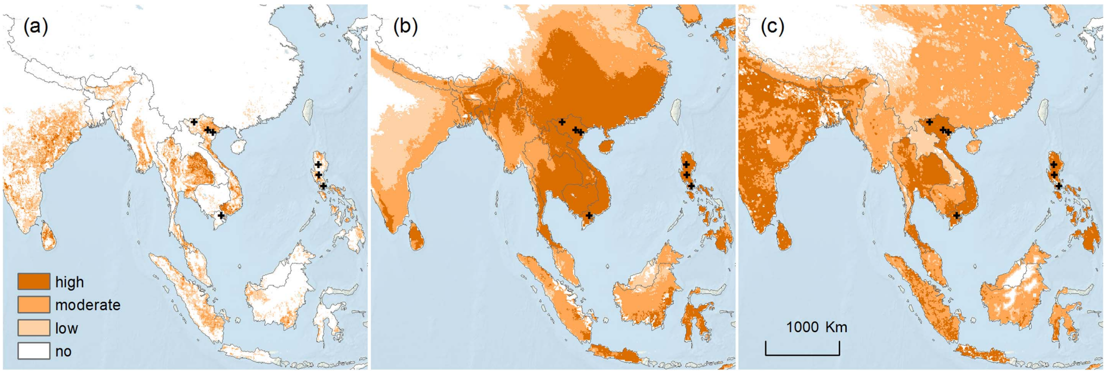

Figure 8. Transferability potential for the LEGATO regional project based on (a) land-use intensity indicators, (b) environmental indicators, and (c) socioeconomic indicators. The black crosses denote locations of the project's seven study landscapes in the Philippines and Vietnam.

are also based on hybrid maps that link remote sensing or ground-based measurements with outputs of mechanistic models, therefore errors in the base data can propagate onto derivative maps (Verburg *et al* 2011). This also explains why many available land use indicators tend to be correlated, although in our analysis we included only those with limited redundancy (table A2). Although we embraced a wide range of variables on land-use intensity as well as environmental and socioeconomic conditions, numerous gaps exist in the availability of important land system indicators. For instance, information on mechanization, farm size, pesticide use, labor intensity, shifting cultivation or forest logging is lacking or is unavailable in adequate quality for many regions. Furthermore, information on culture, governance and policies are notoriously difficult to capture in spatially explicit datasets (Otto *et al* 2015).

On the other hand, our approach is not limited to the selected sets of indicators but allows including any data that are appropriate for a given case study and research question. For example, we included yields for three major crops as output metrics of land-use intensity because together they are representative for the majority of global cereal production. However, data for many other crops are now available. For instance, oil palm and soybean plantations are of major concern for conservation due to their expansion in the tropics (Gasparri *et al* 2013, Wilcove *et al* 2013); they can be used in the analysis in addition to or instead of the current three crops. Our approach also allows giving preference to specific variables or sets of variables. Figure 8 provides an example of the transferability potential analysis for LEGATO calculated separately for land-use intensity, environmental and socioeconomic conditions. For instance, when the environmental conditions are considered to be the sole criteria for defining transferability potentials, the results identify large portion of Southeast Asia as having similar land systems determined by broad-scale gradients of climate, soil and natural productivity of ecosystems (figure 8(b)). When land-use intensity is selected as the main criterion, the areas with high transferability potentials are restricted to a scattered pattern of intensive irrigated cropping systems in the Philippines, Vietnam, Thailand and Indonesia (figure 8(a)). The combination of all sets of variables then leads to the final pattern determined by the overall similarity of land systems to the project archetype (figures 4 and 5).

Transferability, however, is a complex issue and testing which specific results or land management recommendations may be transferable into which regions, and how they can be implemented, requires a separate comprehensive analysis for each case study, based on project-specific hypotheses and fine-scale methods and data. For example, LEGATO investigates how to advance long-term sustainable development of irrigated rice agro-ecosystems, quantifying a range of ecosystem services, from provisioning services of rice production, through regulating services of pollination and biocontrol, to cultural services of identity and sense of place (Settele *et al* 2015). Different sets of criteria would have to be considered to test transferability of findings for different ecosystem services. The transfer of results regarding rice production requires accounting not only for the land-use metrics considered in this study but also for soil characteristics (e.g. concentration of silicon), dynamics of soil biota, varieties of rice planted or co-production of other goods in the rice paddies, such as fish and molluscs (Klotzbücher *et al* 2015, Schmidt *et al* 2015). The transfer of results regarding biological control of pests depends on the functional similarity of local food webs (species compositions, population densities, growth rates) that occur in landscapes with comparable habitat heterogeneity and is restricted to areas where the costs of pesticide application are high enough for farmers to be motivated to search for methods using biocontrol, or where governments intervene to enforce principles of ecological engineering (Spangenberg *et al* 2015). The results regarding cultural services cannot be easily transferred outside of the cultural context defined by the semiotic system of local communities, including religious views, belief systems, traditions and rituals (Spangenberg *et al* 2014). These complex issues illustrate that rather than offering a way to test local-scale transferability of specific findings *per se*, our approach provides a starting point to identify broad-scale regions with potential transferability of place-based research by calculating envelopes that define the general boundaries of projects' relevance outside of their study areas.

5. Conclusions

Place-based research in local and regional case studies has been central to understanding land use as a result of dynamic interactions within SESs that operate across spatial and temporal scales (Rounsevell *et al* 2012). Any generalization of place-based research is challenging because results depend on host of factors unique to the study system. Needed are ways of extracting general insights from the idiosyncrasies of place, so they can be applied to previously unstudied systems (van Vliet *et al* 2015). In this paper, we addressed this challenge by assessing the geographical relevance of case studies and investigated their potential transferability beyond the geographical context in which they are conducted. We adapted the previously developed concept of LSAs because land systems serve as an efficient platform for integrating different perspectives and dimensions of land use research (Verburg *et al* 2015). Our analysis of transferability potentials contributes to the development of globally relevant knowledge creation and sharing in land system science, and advances the discussion on how applicable the most up-to-date global datasets are for characterizing regional-scale findings. The proposed method can serve as a blueprint for large-scale research programs to assess potential transferability of place-based studies to other geographical areas and to indicate possible gaps in research efforts. Such assessments will be ultimately helpful to better understand and enhance the transparency of the biophysical and socioeconomic background on which decision-makers develop and evaluate SLM strategies.

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Appendix 3

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ORIGINAL ARTICLE

Addressing future trade-offs between biodiversity and cropland expansion to improve food security

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Abstract Potential trade-offs between providing sufficient food for a growing human population in the future and sustaining ecosystems and their services are driven by various biophysical and socio-economic parameters at different scales. In this study, we investigate these trade-offs by using a three-step interdisciplinary approach. We examine (1) how the expected global cropland expansion might affect food security in terms of agricultural production and prices, (2) where natural conditions are suitable for cropland expansion under changing climate conditions, and (3) whether this potential conversion to cropland would affect areas of high biodiversity value or conservation importance. Our results show that on the one hand, allowing the expansion of cropland generally results in an improved food security not only in regions where crop production rises, but also in net importing countries such as India and China. On the other hand, the estimated cropland expansion could take place in many highly biodiverse regions, pointing out the need for spatially detailed and context-specific assessments to understand the possible outcomes of different food security strategies. Our multidisciplinary approach is relevant with respect to the Sustainable Development Goals for implementing and enforcing sustainable pathways for increasing agricultural production, and ensuring food security while conserving biodiversity and ecosystem services.

Keywords Cropland expansion · Endemism richness · Land-use change · Crop suitability · Simulation models · Spatial econometrics

Introduction

Halving the proportion of undernourished people in the developing countries by 2015 was one of the objectives of the United Nation's Millennium Development Goals (MDGs). The prevalence of undernourishment was reduced between the periods 1990–1992 and 2012–2014 from 18.7 to 11.3 % globally and from 23.4 to 13.5 % in developing countries in the same period of time (FAO et al. 2014). However, the 2014 MDG report argues that while this target has been met on a global scale, South Asia and sub-Saharan Africa are lacking behind (United Nations 2014). Therefore, the challenge of meeting food security goals is likely to persist in the future.

With a world population that is expected to grow from currently about 6.9–9.2 billion by 2050, as well as

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changing lifestyles and consumption patterns towards more protein-containing diets, global demand for food is projected to increase by 70–110 % by 2050 (Bruinsma 2011; Kastner et al. 2012; Tilman et al. 2011). In order to ensure sufficient food supply in the coming decades, several solutions are suggested. Besides reducing food waste and harvest losses, improving food distribution and access, and shifting diets towards consumption of fewer meat and dairy products, studies conclude that also the increase in global agricultural production is crucially important to meet the increasing demand (Garnett et al. 2013; Godfray et al. 2010; Gregory and George 2011; Gustavsson et al. 2011; Ray and Foley 2013; Mauser et al. 2015). At the same time, agricultural yields as well as production stability are affected by climate change, albeit study results vary between different approaches and assumptions (IIASA and FAO 2012; Rosenzweig et al. 2013; van Ittersum et al. 2013).

The possibilities to increase agricultural production consist of intensification of existing croplands and of their expansion into uncultivated areas, but both options are associated with environmental externalities, including the pollution of surface and groundwater by agrochemicals, unsustainable water withdrawals, and the loss of biodiversity (Foley et al. 2011). Biodiversity loss due to agricultural activities is particularly worrisome because it has consequences for ecosystem functioning, provisioning of ecosystem services, resilience of social–ecological systems, and ultimately the welfare of human societies (Corvalan et al. 2005). These potential trade-offs are clearly reflected in the recently published Sustainable Development Goals (SDGs). They highlight the topic of food security and sustainable agriculture (UN 2012), but compared to the MDGs which were restricted to socio-economic goals, they stress the need to ensure the protection, regeneration and resilience of global and regional ecosystems (ibid §4).

Land-use intensification has been variously shown to negatively impact local biodiversity in many regions of the world (Flynn et al. 2009; Newbold et al. 2015). However, land-use expansion with its associated loss and fragmentation of natural habitats is the globally more dominant driver of biodiversity loss, particularly in highly biodiverse tropical and subtropical regions (Foley et al. 2005; Hosonuma et al. 2012; Pereira et al. 2012). Despite the negative externalities of cropland expansion and continuing calls for sustainable intensification (Garnett et al. 2013; Tilman 1999; West et al. 2014), the future expansion of agricultural land is still considered to be a likely scenario (see, e.g., the OECD/FAO Agricultural Outlook). Land productivity considerably increased over the last decades (FAOSTAT 2015). However, when neglecting future changes in cropping patterns and management, current yield trends of the most important staple crops are not sufficient to double global food production by 2050 (Ray et al. 2013). According to FAO, cropland is expected to globally expand by 7 % until 2030 (Alexandratos and Bruinsma 2012). Consequently, it is crucially important to examine (1) how the expected global cropland expansion might affect food security in terms of agricultural production and prices, (2) where natural conditions are suitable for cropland expansion under changing climate conditions, and (3) whether this potential conversion to cropland would affect areas of high biodiversity value or conservation importance. Answering these questions requires a scientific analysis of the trade-offs between achieving food security via cropland expansion on the one hand and conserving biodiversity on the other.

In this study, we investigate the trade-offs between providing sufficient food in the future and sustaining biodiversity by using a three-step interdisciplinary approach. First, we examine the impact of cropland expansion on food security in terms of agricultural production quantity and prices. In the following step, we identify areas that are biophysically most suitable for the potential expansion of cropland under specific climate scenario conditions. Finally, we use information on global patterns of endemism richness, in order to identify hot spots where biodiversity could be most affected by potential cropland expansion.

Methods and data

We use three different approaches to analyse trade-offs between food security and biodiversity since they are driven by various interdependent socio-economic and biophysical parameters that operate at different spatial scales. First, to address the impact of cropland expansion on global and regional agricultural markets we apply the computable general equilibrium model DART-BIO. The model accounts for socio-economic developments such as population growth and changes in consumption patterns, while it considers repercussions between different production sectors and regions, simulating the development of food quantity and prices as important indicators for food security. Second, since this approach does not allow for localizing cropland expansion, we use biophysical drivers at the local scale such as climate, soil quality, and topography to determine where an expansion of cropland potentially would be possible under the given natural conditions. Third, we use data on endemism richness, a biodiversity metric that represents the importance of an area for conservation, to statistically examine the spatial concordance between patterns of global biodiversity and potential cropland expansion.

The DART-BIO model

The Dynamic Applied Regional Trade (DART) model is a multi-sectoral, multi-regional recursive dynamic computable general equilibrium (CGE) model of the world economy. The DART model has been applied to analyse international climate policies (e.g. Springer 1998; Klepper and Peterson 2006a), environmental policies (e.g. Weitzel et al. 2012), energy policies (e.g. Klepper and Peterson 2006b), and agricultural and biofuel policies (e.g. Kretschmer et al. 2009) among others.

The DART model is based on data from the Global Trade Analysis Project (GTAP) covering multiple sectors and regions. The economy in each region is modelled as a competitive economy with flexible prices and market-clearing conditions. The dynamic framework is recursively dynamic, meaning that the evolution of the economies over time is described by a sequence of single-period static equilibria connected through capital accumulation and changes in labour supply. The economic structure of DART is fully specified for each region and covers production, investment, and final consumption by consumers and the government.

DART is calibrated to the GTAP8 database (Narayanan et al. 2012) that represents production and trade data for 2007 with input–output tables for the world economy. The particular version used here (DART-BIO) contains 45 sectors and has detailed features concerning the agricultural sectors. Thirty-one activities in agriculture (thereof ten crop sectors) are explicitly modelled which represent a realistic picture of the complex value chains in agriculture. Several sectors that are only available on an aggregated level in the GTAP database are therefore split. The regional aggregation of 23 regions is chosen to include countries where main land use changes either due to biofuels production or because major changes in population, income, and consumption patterns are expected to emerge (e.g. Brazil, Malaysia, China). A detailed model description of the database and data processing can be found in Calzadilla et al. (2014).

In the DART-BIO model, we use different land types according to agro-ecological zones (AEZs), based on the GTAP database. AEZs represent 18 types of land, in each region with different crop suitability, productivity potential, and environmental impact. Each of the 18 AEZs is characterized by its particular climate, soil moisture/precipitation, and landform conditions which are basic for the supply of water, energy, nutrients, and physical support to plants. The newest version is available in the GTAP8 database by Baldos and Hertel (2012).

The mobility of land from one land-use type to another is commonly restricted by a nested constant elasticity of transformation (CET) function (see, e.g., Laborde and Valin 2012; Hertel et al. 2010). We choose a three-level nesting, in which land is first allocated between land for agriculture and managed forest. Then, agricultural land is allocated between pasture and crops. In the next level, cropland is allocated between rice, palm, sugar cane/beet and annual crops (wheat, maize, rapeseed, soybeans, other grains, other oilseeds, and other crops). At each level, the elasticity of transformation increases, reflecting that land is more mobile between crops than between forestry and agriculture (see Appendix Table 2). An important difference compared with other approaches (e.g. Laborde and Valin 2012; Bouët et al. 2010) is that we do not differentiate between land prices for growing annual crops. Since farmers can decide year by year which crop to plant, these crops can be easily substituted depending mainly on crop prices. Thus, different annual crops (e.g. wheat and maize) face only one land price entering into their costs. However, paddy rice and perennial crops such as palm fruit and sugar cane are less mobile and therefore face different land prices. Elasticities of transformation between the land uses are the main drivers of land allocation; however, they are very poorly studied in the literature. We currently use numbers from OECD's PEM model (Abler 2000; Salhofer 2000) which only covers developed countries plus Mexico, Turkey, and South Korea. Therefore, we had to choose values based on certain similarities for several countries (see Appendix Table 2). The effect of differences in land-use modelling is discussed in Calzadilla et al. (forthcoming).

Productivity in the agricultural sector is determined by changes in labour force, the rate of labour productivity growth, and the change in human capital accumulation, as well as the choice of the model structure (e.g. CET nesting) and parameter settings (e.g. elasticity of substitution). Hence, future yield growth is driven by changes in the total productivity factor. A more detailed description of production functions and dynamics is available in Calzadilla et al. (2014).

To simulate the effect of cropland expansion on food security, we set up two scenarios. The *baseline scenario* represents a continuation of the business as usual economic growth, population growth, and national policies as observed in the DART-BIO 2007 database. In this reference scenario, no expansion of cropland into non-managed land types is assumed.

The assumptions underlying the *land expansion (LE) scenario* are based on the FAO long-term baseline outlook 'World agriculture: towards 2030/2050'—The 2012 Revision (Alexandratos and Bruinsma 2012). These reports are the most authoritative sources for forecasts on crop production available. The forecasts are based on annual growth rate projections until 2030/2050 for crop production for selected important food crops.

From the information provided in the FAO forecast, we calculate annual growth rates for a linear increase in

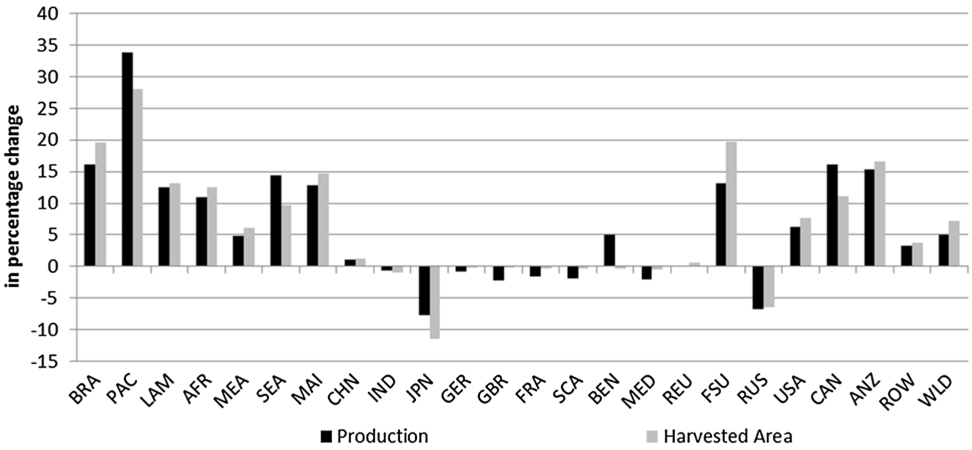

Fig. 1 Percentage change in global crop production under the land expansion scenario and harvested area in 2030 compared with 2007. *Source* simulation of production with DART-BIO; harvested area based on Alexandratos and Bruinsma (2012)

harvested area from the 2005/2007 base years, as provided by the FAO to 2030 (assumptions on growth rates include the most important crops cultivated on cropland). They enter the DART-BIO model as exogenous parameters. Globally, harvested area is expected to increase by about 7 %, while the regional distribution of land expansion or contraction varies between contraction of cropland (e.g. −11 % in Japan) and expansion of up to 28 % in Paraguay/Argentina/Uruguay/Chile (PAC) (Fig. 1 and Appendix Fig. 5). Accordingly, the land endowment for agricultural production in the DART-BIO model is set to consider these differences. While in northern and middle Europe, China, and India the harvested area shows no significant changes over time, the harvested area in Japan and Russia is reduced. The FAO data (Alexandratos and Bruinsma 2012) show that largest land expansions occur in Latin America (BRA, PAC, LAM) and Rest of Former Soviet Union and Europe (FSU).

Natural potentials for future cropland expansion

The potential for the expansion of cropland is restricted by the availability of land resources and given local natural conditions. Consequently, area that is highly suitable for agriculture according to the prevailing local ecological conditions (climate, soil, terrain) but is not under cultivation today has a high natural potential for being agriculturally used. Policy regulations or socio-economic conditions can further restrict the availability of land for expansion, e.g., by designating protected areas, although they may be suitable for agriculture. Conversely, by applying, e.g., irrigation practices, land can be brought under cultivation, although it may naturally not be suitable. Here, we investigate the potentials for agricultural expansion for near future climate scenario conditions to identify the suitability of non-cropland areas for expansion.

We determine the available energy, water, and nutrient supply for agricultural suitability from climate, soil, and topography data, by applying the global dataset of crop suitability from a fuzzy logic approach by Zabel et al. (2014). It considers 16 economically important staple and energy crops at a spatial resolution of 30 arc seconds. These are barley, cassava, groundnut, maize, millet, oil palm, potato, rapeseed, rice, rye, sorghum, soy, sugarcane, sunflower, summer wheat, and winter wheat. The parameterization of the membership functions that describe each of the crops' specific natural requirements is taken from Sys et al. (1993). The considered natural conditions are: climate (temperature, precipitation, solar radiation), soil properties (texture, proportion of coarse fragments and gypsum, base saturation, pH content, organic carbon content, salinity, sodicity), and terrain (elevation, slope). The requirements for temperature and precipitation are defined over the growing period. For this case, we calculate the optimal start of the growing period, considering the temporal course of temperature and precipitation and thus the course of dry and rainy seasons.

As a result of the fuzzy logic approach, values in a range between 0 and 1 describe the suitability of a crop for each of the prevailing natural conditions at a certain location. The smallest suitability value over all parameters finally determines the suitability of a crop. The daily climate data (mean daily temperature and precipitation sum) are provided by simulation results from the global climate model ECHAM5 (Jungclaus et al. 2006) for near future (2011–2040) SRES A1B climate scenario conditions. Soil data are taken from the Harmonized World Soil Database (HWSD) (FAO et al. 2012), and topography data are applied from the Shuttle Radar Topography Mission (SRTM) (Farr et al. 2007). In order to gather a general crop suitability, which does not refer to one specific crop, the most suitable crop with the highest suitability value is chosen at each pixel. Thus, we create a potential land use for each pixel, based on the most suitable crops. This land use does not refer to actual land use and the actual allocation of crops but is used for the further calculation of natural expansion potential.

In addition to the natural biophysical conditions, we consider today's irrigated areas based on Siebert et al. (2013). We assume that irrigated areas globally remain constant until 2040, since adequate spatial data on possible future extend of irrigated areas do not exist, although it is likely that freshwater availability for irrigation could be limited in some regions, while in other regions surplus water supply could be used to expand irrigation practices (Elliott et al. 2014). However, it is difficult to project where irrigation practices will evolve, since it is also driven by economic considerations, such as the amount of investment costs that are required to establish irrigation infrastructure.

In principle, all agriculturally suitable land that is not used as cropland today has the natural potential to be converted into cropland. We assume that only urban and built-up areas are not available for conversion, although more than 80 % of global urban areas are agriculturally suitable (Avellan et al. 2012). However, it seems unlikely that urban areas will be cleared at the large scale due to high investment costs, growing cities, and growing demand for settlements. Concepts of urban and vertical farming usually are discussed under the aspects of cultivating fresh vegetables and salads for urban population. They are not designed to extensively grow staple crops such as wheat or maize for feeding the world in the near future. Urban farming would require one-third of the total global urban area to meet only the global vegetable consumption of urban dwellers (Martellozzo et al. 2015). Thus, urban agriculture cannot substantially contribute to global agricultural production of staple crops and consequently is not considered in this study.

Protected areas or dense forested areas are not excluded from the calculation, in order not to lose any information in the further combination with the biodiversity patterns (see chapter 2.3). We use data on current cropland distribution by Ramankutty et al. (2008) and urban and built-up area according to the ESA-CCI land-use/land-cover dataset (ESA 2014). From these data, we calculate the 'natural expansion potential index' (I_{exp}) that describes the natural potential for an area to be converted into cropland as follows:

$$I_{\mathrm{exp}} = S \times A_{\mathrm{av}}$$

The index is determined by the quality of crop suitability (S) (values between 0 and 1) multiplied with the amount of available area (A_{av}) for conversion (in percentage of pixel area). The available area includes all suitable area that is not cultivated today and not classified as urban or artificial area. The index ranges between 0 and 100 and indicates where the conditions for cropland expansion are more or less favourable, when taking only natural conditions into account, disregarding socio-economic factors, policies, and regulations that drive or inhibit cropland expansion.

Since it is unknown which crop might be used for expansion, the index uses the most suitable crop at each pixel (as given by the general crop suitability) for determining the natural potential for expansion. Consequently, not all crops might be suitable for expansion where I_{exp} is greater than zero. The index is a helpful indicator for identifying areas where natural conditions potentially allow for expansion of cropland in the near future from a biophysical point of view. The index does not allow for determining the likelihood of cropland expansion, since it ignores socio-economic factors and policy regulations because we do not aim to understand the factors that may affect cropland expansion. Rather, our goal is to localize potential conflicting areas.

Trade-offs between biodiversity and potential cropland expansion

As indicators of biodiversity, we use global endemism richness for birds, mammals, and amphibians created from expert-based range maps obtained from the International Union for Conservation of Nature (IUCN 2012) and Birdlife databases (BirdLife 2012). Habitat changes due to cropland expansion are the principal driver of extinction risk in these animal groups (Pereira et al. 2012). We choose endemism richness over other biodiversity indicators because it combines species richness with a measure of endemism (i.e. the range sizes of species within an assemblage) and thus indicates the relative importance of a site for global conservation (Kier et al. 2009). We calculate endemism richness as the sum of the inverse global range sizes of all species present in a grid cell. The data are scaled to an equal area grid of 110 × 110 km at the equator (1 arc degree) because at finer spatial resolutions, the underlying species range maps exhibit excessively high false-presence rates, overestimating the area of occupancy of individual species (Hurlbert and Jetz 2007).

Following similar methods as in Kehoe et al. (2015), we overlay endemism richness indicators with the natural expansion potential index to examine the spatial concordance between patterns of global biodiversity and suitability for cropland expansion. First, we statistically quantify the spatially explicit association between endemism richness and cropland expansion potentials using the bivariate version of the local indicator of spatial association (LISA) (Anselin 1995). LISA represents a local version of the correlation coefficient and shows how the nature and strength of the association between two variables vary across a study area. The method allows for the decomposition of global indicators, such as Moran's I, into the contribution of each individual observation (e.g. a grid cell), while giving an indication of the extent of significant spatial clustering of similar values around that observation. Using OpenGeoDa version 1.2.0 (Anselin et al. 2006), we calculate the local Moran's I statistic of spatial association for each 110-km grid cell as:

$$I_i = \frac{x_i - \bar{x}}{s^2} \sum_{j=1, j \neq i}^{n} w_{ij}\left(y_j - \bar{y}\right)$$

where x_i and y_j are standardized values of variable x (e.g. cropland expansion potentials) and variable y (e.g. endemism richness) for grid cells i and j, respectively, $\bar{x}$ and $\bar{y}$ are the means of the variables, w_{ij} is the spatial weight between cell i and j inversely proportional to Euclidean distance between the two cells, and s^2 is the variance. Based on the values of local Moran's I, we identify and map spatial associations of (1) high–high values, that is spatial hot spots in which locations with high values of cropland expansion potentials are surrounded by high values of endemism richness, (2) low–low values, that is spatial cold spots in which locations with low values of cropland expansion potentials are surrounded by low values of endemism richness, and (3) high–low and low–high values, where the spatial association between the variables is negative (inverse). The strength of the relationship is measured at the 0.05 level of statistical significance calculated by a Monte Carlo randomization procedure based on 499 permutations (Anselin et al. 2006). We use the resulting areas of high–high values to generate a summary map of high-pressure regions for all three taxonomic groups (birds, mammals, and amphibians). As a second analysis, we delineate the 'hottest' hot spots of high cropland expansion potentials and endemism richness by extracting the top 5 and 10 % of the data distribution (Ceballos and Ehrlich 2006). Intersecting these top values of both variables, we create maps of the top pressure regions, where high biodiversity is most threatened by potential cropland expansion.

Results and discussion

The impact of cropland expansion on food security

Food supply and accessibility depend not only on the ability to produce a sufficient quantity and quality of food, but also on the food price level and incomes relative to these prices. We apply the CGE Model DART-BIO in order to compare agricultural production and prices on global and regional scale under two scenarios. The land expansion (LE) scenario (cp. "The DART-BIO model") is run and compared to results from a baseline scenario without cropland expansion to quantify the price and production changes. To illustrate the effect of expanding cropland on food security, first the changes in global and regional production quantities and trade flows are displayed. Second, changes in price on global and regional scale under the LE scenario are discussed.

Food production and trade flows

Under the LE scenario, global production of primary agricultural goods increases by 3–9 %, while processed food production rises by 3 % compared with the baseline scenario in 2030. A detailed table with price and quantity changes for all crops and processed food sectors is available in Appendix Table 3.

Regionally, the cropland expansion has different impacts on food production. Driven by the amount in cropland expansion/reduction of the scenario, crop production in European countries except Benelux as well as in Russia, Japan, and India is reduced in 2030 compared with 2007 (see Fig. 1). Largest increases in crop production are simulated for Paraguay, Argentina, Uruguay, Chile (PAC) (+34 %), and other regions that face problems in improving food security (Brazil +16 %, LAM +13 %, AFR +11 %, SEA +14 %). Comparing production in 2030 under the LE scenario to the baseline scenario, production of maize, soy beans, and wheat shows largest increase in Latin America. South-East Asia (SEA) and Malaysia/Indonesia (MAI) increase paddy rice production by 11–13 %, while also 'Rest of Agriculture' (AGR) rises considerably. Production of, e.g., wheat and AGR in India drops, since expansion potentials are very limited. These results indicate that while food production rises on global average, not all regions produce more under the LE scenario. Thus, their ability to produce a sufficient quality of food is not improved when expanding cropland as under the LE scenario.

Countries are connected via bilateral trade. Different values for cropland expansions result in changing comparative advantages of different regions, which affects trade flows. In 2030, regions in Asia are net importers of most agricultural goods in the baseline scenario. South-East Asia (SEA) reduces its net imports of processed food by more than half under the LE scenario compared with the baseline. At the same time, SEA exports more AGR (+63 %). These exports mainly target India and China, who also increase imports from other regions. Indian's net imports of crops strongly increase such that private consumption of food in India rises. Regions in Latin America are net exporters of crops and net importers of processed food under the baseline scenario in 2030. Under the LE scenario, net exports of crops increase compared with the baseline, while less processed food is imported. This indicates that cropland expansion, though distributed differently in different regions, provides more food to consumers in all regions compared with the baseline run.

Food prices

Agricultural prices are also important for food security, particularly for net importing countries, and people who do not produce food themselves. Comparing results of the LE scenario with the baseline, global average prices of crops fall by 6–20 % (see Table 3 in Appendix). The highest price decreases are simulated for soy beans, since they are produced in regions with the highest cropland expansions. In addition, by 2030 the demand for soy beans is larger compared with, e.g., paddy rice as soy beans are used as feedstuff to satisfy rising meat consumption over time, and biofuel quotas. As a result, soybean areas expand by 13 % compared with the baseline run. The area expansion for paddy rice amounts to 5 %, which results in a global average price decrease of 6 %.

Driven by the scenario assumptions, regional production costs, and trade flows, regional price changes vary considerably. Taking wheat as an example, strongest price decreases are simulated for Brazil and PAC, where most of the cropland expansion takes place (see Table 1). But also regions in which cropland does not expand or only to a limited degree profit from decreasing crop prices. While, e.g., wheat production in India decreases under the LE scenario compared with the baseline in 2030, wheat prices drop by 5 % since India benefits from low wheat prices on the world market (−11 %) (see Table 1).

Table 1 Percentage change in wheat prices

Regions	Price change %	Regions	Price change %
BRA	−24.0	SCA	−9.7
PAC	−24.2	BEN	−13.2
LAM	−18.3	MED	−10.3
AFR	−18.1	REU	−11.0
MEA	−13.4	FSU	−22.9
SEA	−12.3	RUS	−1.7
CHN	−6.4	USA	−17.7
IND	−5.0	CAN	−18.5
JPN	5.3	ANZ	−23.9
GER	−10.9	ROW	−12.3
GBR	−11.2	WLD	−11.4
FRA	−9.6		

South America Brazil (BRA); Paraguay, Argentina, Uruguay, Chile (PAC); Rest of Latin America (LAM); *Africa* sub-Saharan Africa (AFR); Middle East, North Africa (MEA); *Asia* South-East Asia (SEA); China (CHN); India (IND); Malaysia, Indonesia (MAI); Japan (JPN); Russia (RUS); Rest of Former Soviet Union and Europe (FSU); *Europe* Germany (GER); UK, Ireland (GBR); France (FRA); Finland, Sweden, Denmark (SCA); Belgium, Netherlands, Luxemburg (BEN); Spain, Portugal, Italy, Greece, Malta, Cyprus (MED); Rest of European Union (REU); *North America and Rest* USA (USA); Canada (CAN); Australia, New Zealand (ANZ); Rest of the World (ROW); global average (WLD)

In summary, our results indicate that cropland expansion improves food security, particularly in those regions that currently face problems in providing sufficient and affordable quantities of food to people. However, data from FAO used in the LE scenario provide no spatial information on the locations within the regions where expansion takes place. Accordingly, no statement on substituted land cover and possible loss of biodiversity is possible. Therefore, in the following section, potential areas for cropland expansion are identified.

Identification of natural potentials for cropland expansion

Assuming that cropland expansion is potentially possible where the quality of land is suitable for the cultivation of crops and area is still available for the conversion of land into cropland, Fig. 2 shows the calculated index of the natural expansion potential. The greater the agricultural suitability and the larger the available area for expansion, the greater the value of the index. Red coloured areas in Fig. 2 indicate high natural potential for cropland expansion.

We identify high natural expansion potentials in African countries (e.g. Cameroon, Chad, Gabon, Sudan, western parts of Ethiopia, and Tanzania), Central and South America (Mexico, Nicaragua, Uruguay, and parts of Argentina), fragmented parts of Asia (north-eastern part of China, northern parts of Australia and Papua New Guinea) and small parts of Russia. These areas are characterized by fertile soils and adequate climate conditions for at least one of the investigated crops, while at the same time these areas are not under cultivation today according to the applied data. The high expansion potential in parts of tropical countries, such as Cameroon, Gabon, Nicaragua, Indonesia, Malaysia, Papua New Guinea, and the Philippines, is mainly caused by the high crop suitability of oil palm in these regions, while other crops are not suitable here (Zabel et al. 2014). Regions with high natural expansion potential in the Sahel Zone mainly owe their high values to the good suitability of sorghum.

Certainly, many of the named regions with high natural potential for expansion are in the focus of cropland expansion and land grabbing already today. While the inner tropical basins of Brazil and the Congo show large areas for possible expansion, the value for the expansion potential index is relatively low here, since the agricultural suitability is inhibited due to marginal soil quality conditions. On the other hand, the potential for expansion is

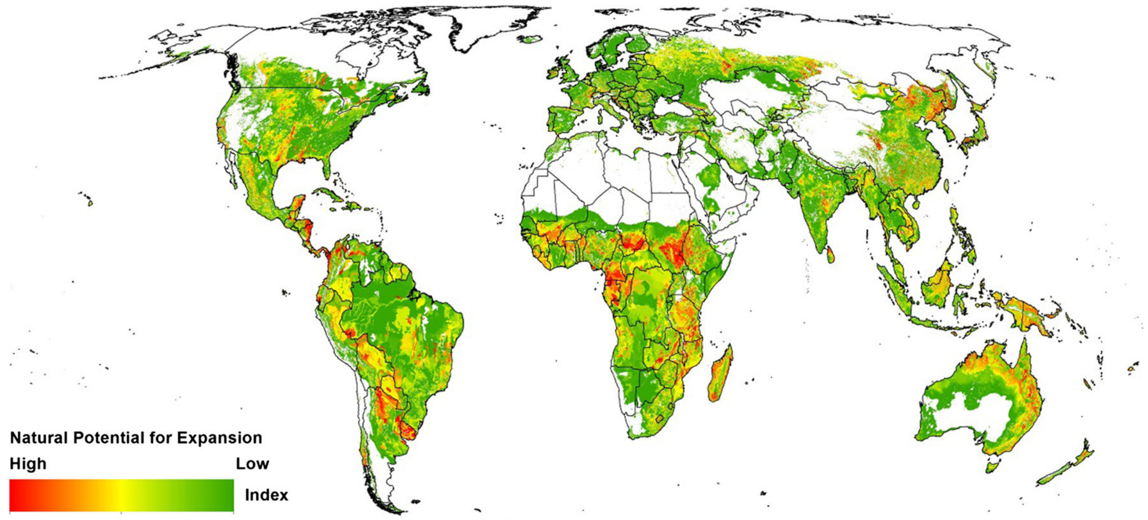

Fig. 2 Index of natural potentials for the expansion of cropland. The index is calculated as the result of agricultural suitability under SRES A1B climate scenario conditions for 2011–2040 and the availability of suitable land for expansion. The index ranges from 1 (low potential for expansion, *green*) to 100 (high potential for expansion, *red*). Values with 0 (no potential for expansion) are masked out. *Map* in Eckert IV projection, 30-arc-second spatial resolution

relatively low in North America and Europe, where most of the suitable areas are already under cultivation today. Therefore, the potential for further expansion is relatively low. Topography also affects agricultural suitability, and thus, the natural potential for expansion depends also on the extent of suitable valleys within mountainous areas.

Increasing mean temperatures due to climate change until 2040 are considered in the calculation of natural expansion potentials. Climate change, e.g., affects the northern hemisphere, where the climatic frontier for cultivation shifts northwards with time such that additional land potentially becomes suitable and thus is available for expansion. On the other hand, suitability decreases for most of the 16 investigated crops due to climate change, especially for cereals in the tropics and the Mediterranean.

Spatial patterns of potential cropland expansion and biodiversity

The LISA analyses reveal regionally variable spatial concordance between patterns of cropland expansion potentials and global biodiversity (Fig. 3). Regions with low potential of cropland expansion and low biodiversity (i.e. spatial cold spots) are similar across all three taxonomic groups, covering mostly non-arable, desert, or ice-covered land (39 % of terrestrial ecosystems; Fig. 3a–c). The hot spots, i.e. regions where high biodiversity is potentially threatened by cropland expansion, vary more substantially among the considered vertebrate groups but all are focused primarily in the tropics, covering 18 % of the terrestrial land surface. While the hot spot patterns for birds and mammals show high spatial congruence (67 % overlap), the areas of high expansion potentials associated with high endemism richness are relatively smaller for amphibians (41 % overlap with the other taxa) due to the generally smaller ranges of amphibian species concentrated in specific geographical areas. However, the summary of statistically significant hot spots for all three taxonomic groups shows a spatially consistent pattern of high-pressure regions (Fig. 3d), covering Central and South America, Central Africa and Madagascar, Eastern Australia, and large portions of Southeast Asia. Other regions with higher suitability for cropland expansion either are not significantly associated with endemism richness or occur in areas with relatively low levels of endemism richness (11 % of the terrestrial land surface), e.g. the Midwest of North America, Eastern Europe, or parts of sub-Saharan Africa.

The spatial intersect of the top 5 and 10 % of data on cropland expansion and biodiversity (Fig. 4) further pinpoints the top pressure regions, where high levels of endemism richness for all considered taxa may be most threatened by potential cropland expansion (3 % overlap for top 5 % data and 13 % overlap for top 10 % data). These ‘hottest’ hot spots of potential future conflict between biodiversity and agriculture are found in Central America and the Caribbean, in the tropical Andes and south-western Brazil, in West and East Africa, including Madagascar, and in several parts of tropical Asia, in particular the Indochina region, the Indonesian islands, and Papua New Guinea.

Although our results highlight relatively large areas of potential future pressure on biodiversity, it does not mean

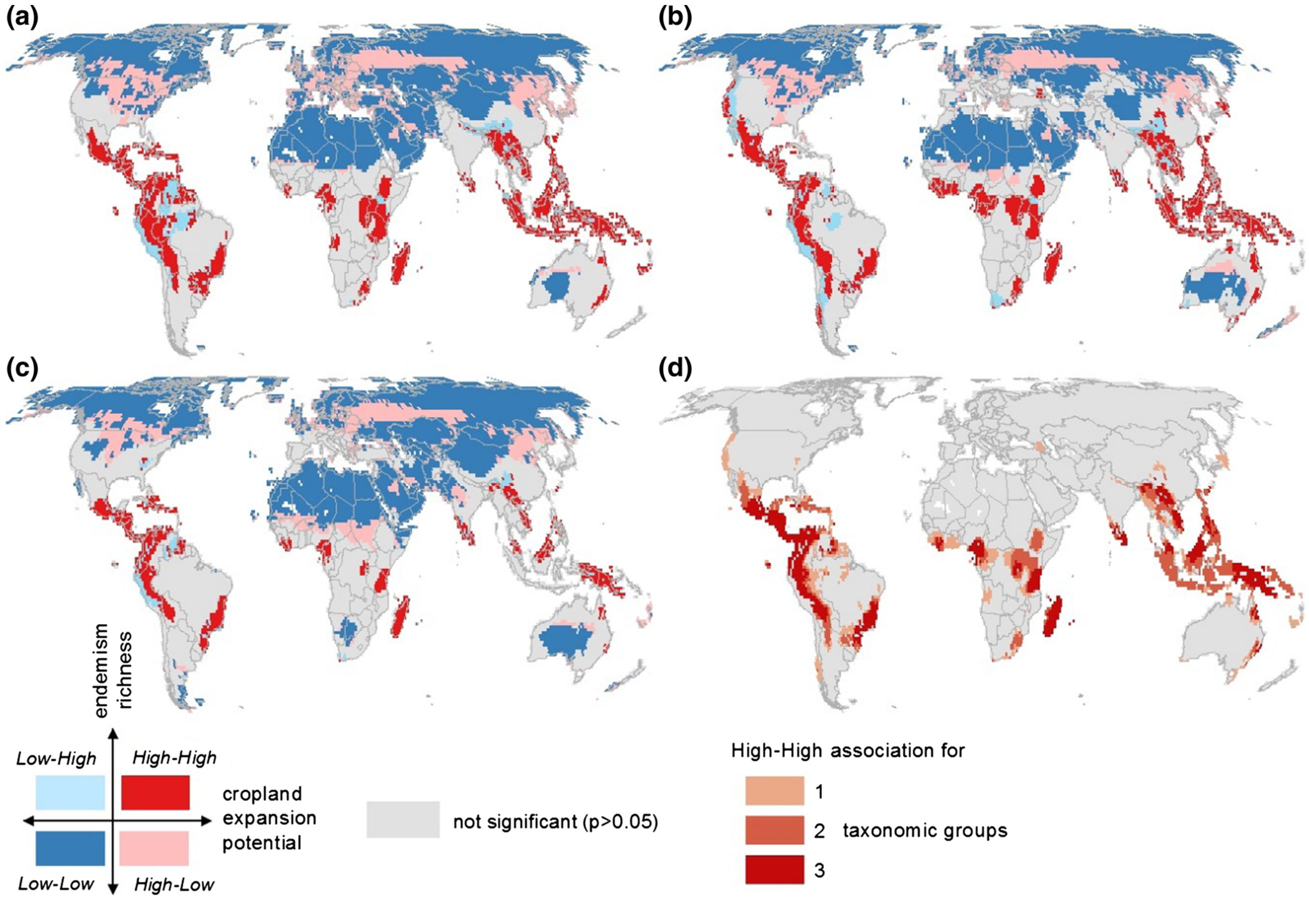

Fig. 3 Local indicator of spatial association (LISA) between cropland expansion potentials and endemism richness for birds (**a**), mammals (**b**), and amphibians (**c**). The pattern shows how the nature and strength of the association between two variables vary across the globe. High–high clusters show hot spot locations, in which high cropland expansion potentials are associated with high values of endemism richness. Low–low clusters show cold spot locations, in which low cropland expansion potentials are associated with low values of endemism richness. High–low and low–high clusters show inverse spatial association. The *map* in (**d**) summarizes all high–high associations to show high-pressure regions for one, two, or all three taxonomic groups. *Maps* in Eckert IV projection, 1-arc-degree spatial resolution

that all types of habitats in each 110-km grid cell would be equally affected if cropland expansion occurred. When using endemism richness as an indicator of biodiversity, our concern is not the area of habitat but the number of range equivalents, i.e. fractions of species global ranges that are contained within a grid (Kier et al. 2009). For example, many mountainous regions in the tropics identified as high-pressure regions have high endemism richness due to many different species inhabiting zones along topographical and climate gradients. Presumably, the habitats in higher elevations are less likely to be affected than habitats located in lower regions because of differences in soil characteristics, slope steepness, accessibility, and other fine-scale factors restricting agricultural suitability and thus natural expansion potential in mountainous areas.

On the other hand, we also identify areas where high suitability for additional expansion of food production may pose lower threats to conservation of biodiversity. These regions, such as Eastern Europe, sub-Saharan Africa, or Northeast China, coincide with the ‘extensive cropping land system’ (Václavík et al. 2013) that represents relatively easily achievable opportunity for an expansion or intensification of agricultural production, especially for wheat, maize, or rice. Here, large production gains could be achieved if yields were increased to only 50 % of attainable yields (Mueller et al. 2012). However, even areas with relatively low endemism richness may still harbour valuable species or include cultural heritage that cropland expansion may threaten. Our analysis identifies where the high- and low-pressure regions are located but does not explain how the various aspects of biodiversity would be threatened by future land-use changes. Therefore, we caution that more detailed and context-specific assessments are needed to understand the possible outcomes of different expansion strategies. In addition to biodiversity and economic indicators, these assessments should consider other

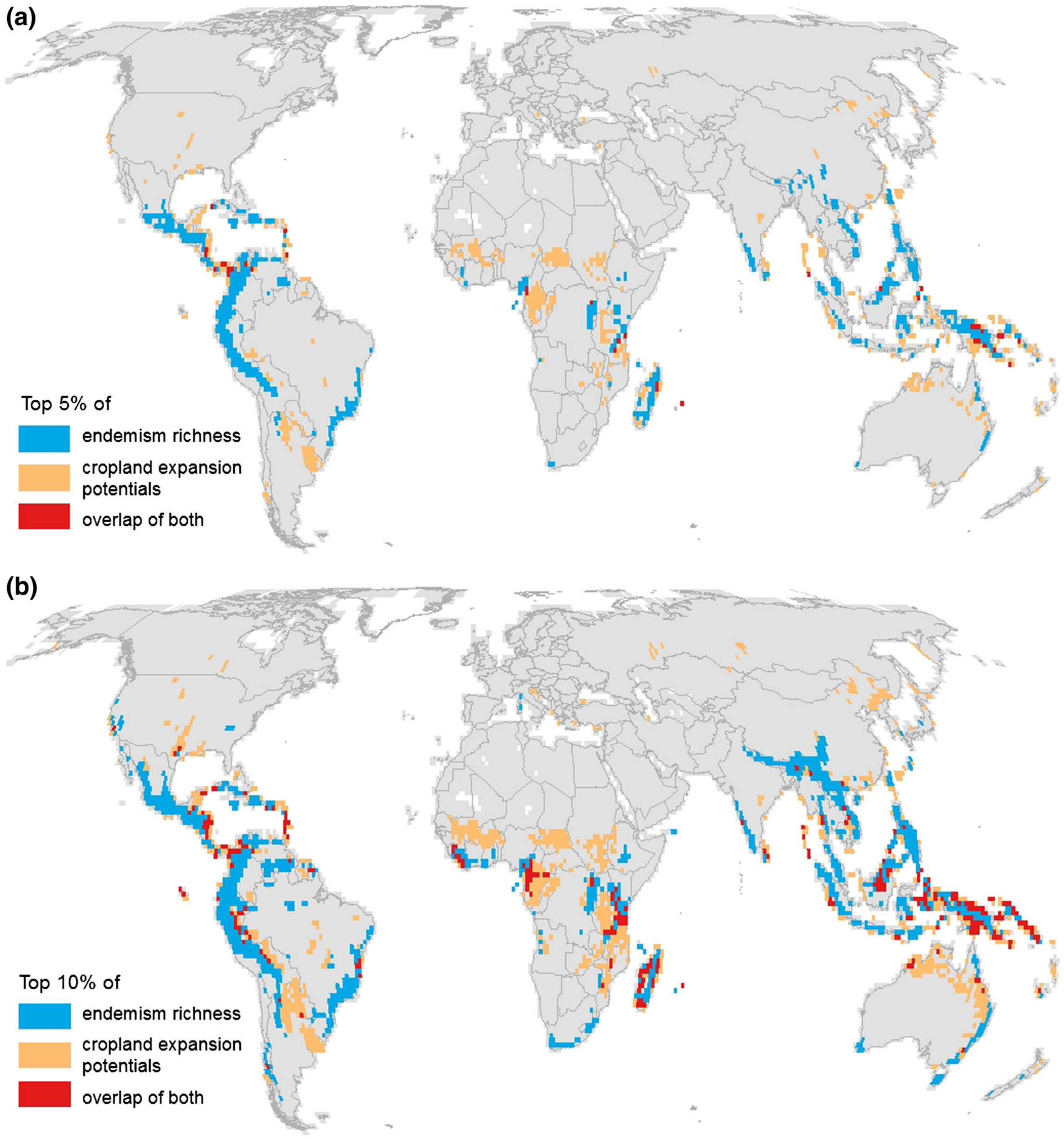

Fig. 4 Overlay of top 5 % (**a**) and top 10 % (**b**) of natural cropland expansion potentials and global endemism richness for three vertebrate taxa (birds, mammals, and amphibians). The intersect of both datasets (in *red*) highlights the top pressure regions, where high biodiversity (i.e. high numbers of range size equivalents) may be particularly threatened by potential cropland expansion. *Maps* in Eckert IV projection, 1-arc-degree spatial resolution

(non-provisioning) ecosystem services, resilience of land-use systems, and cultural and societal outcomes of increasing food production (Kehoe et al. 2015).

Summary and conclusions

Trade-offs between food security and biodiversity are driven by various interdependent socio-economic and bio-physical parameters that operate at both global and local scales. In this study, we account for these parameters by combining three methodological approaches to analyse the effects of expanding agricultural production: (1) we run an economic scenario analysis with a computable general equilibrium model to examine the effect of an exogenous cropland land expansion on changes in crop production and prices, (2) we determine where an expansion of cropland would be possible under the given natural conditions, and (3) we statistically analyse where the natural potential for cropland expansion may threaten biodiversity.

We show that there are potential trade-offs between increased food production and protection of biodiversity. On the one hand, allowing the expansion of cropland generally results in improved food security in terms of decreased food prices and increased quantity, not only in those regions where crop production rises, but also in net importing countries such as India and China. On the other hand, the results show that estimated cropland expansion could take place in many regions that are valuable for biodiversity conservation. From an economic point of view, the highest expected expansion of cropland according to FAO takes place in South America, particularly in Argentina, Bolivia, and Uruguay. Considering that these countries also have a high biophysical potential for cropland expansion as well as relatively high endemism richness, they represent valuable regions from the conservation point of view but with the highest pressure for land clearing. Similar conclusions can be made for regions in Australia, Brazil, and Africa. Our analyses highlight such regions that deserve further attention and more detailed and context-specific assessments to understand the possible outcomes of different food security strategies, while at the same time establishing mechanisms to efficiently protect habitats with high biodiversity.

Our results are relevant with respect to the SDGs for implementing and enforcing sustainable pathways for increasing agricultural production, ensuring food security while conserving biodiversity and ecosystem services. A report by the International Council for Science (ICSU) and the International Social Science Council (ISSC) states that some goals may conflict. The presented approach contributes to identifying the key trade-offs and complementarities among goals and targets, as required in SDGs. In addition, our study contributes to the land sharing versus sparing debate that generated a controversial discussion on the pressing problems of feeding a growing human population and conserving biodiversity (Fischer et al. 2008; Godfray 2011; Phalan et al. 2011; von Wehrden et al. 2014). Our approach represents one of the first examples of moving forward from the bipolar framework (Fischer et al. 2014). We advance the framework by (1) accounting for economic parameters, thus focusing on food security rather than mere production, (2) treating agricultural landscapes as complex social–ecological systems, (3) accounting for biophysical and socio-economic factors that operate at different spatial scales, and (4) defining biodiversity with a metric that combines species richness with conservation value of the area.

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Appendix 4

Ecosystem Services 28 (2017) 273–282

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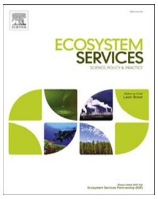

Integrating ecosystem service bundles and socio-environmental conditions – A national scale analysis from Germany

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ABSTRACT

Understanding the relationship and spatial distribution of multiple ecosystem services (ES) in the context of underlying socio-environmental conditions is an essential element of national ecosystem assessments. Here, we use Germany as an example to present a reproducible blueprint approach for mapping and analysing ecosystem service bundles (ESB) and associated socio-environmental gradients. We synthesized spatial indicators of eleven provisioning, regulating and cultural ES in Germany and used the method of self-organizing maps (SOM) to define and map ESBs. Likewise, we collated data from 18 covariates to delineate socio-environmental clusters (SEC). Finally, we used an overlap analysis to characterise the relationship between the spatial configuration of ESBs and co-occurring SECs. We identified and mapped eight types of ESBs that were characterized to varying degrees by provisioning, cultural and regulating/maintenance services. While ESBs dominated by provisioning ES were linked to regions with distinct environmental characteristics, cultural ESBs were associated with areas where environmental and socio-economic gradients had similar importance. Furthermore, spatial stratification of ESBs indicated hot spots where more detailed analysis is needed within national assessments. Our approach can serve as a blueprint for ESB analysis that can be reproduced in other geographical and environmental settings.

1. Introduction

Since the *Millennium Ecosystem Assessment* (MA, 2005), ecosystem services (hereafter ES) have received increasing attention in science and public to safeguard human livelihood and biodiversity. This is reflected in *The Strategic Plan for Biodiversity 2011–2020* of the *Convention on Biological Diversity* (CBD, 2010), e.g. in the Aichi target goal D aiming to "enhance the benefits to all from biodiversity and ecosystem services" on a global scale. Furthermore the *Intergovernmental Platform on Biodiversity and Ecosystem Services* (IPBES, 2017) was founded to improve the science-policy exchange and to support assessments in this area. At the European scale the *EU Biodiversity Strategy to 2020* (European Commission, 2011) declares the aim of maintaining and restoring ecosystems to ensure the continuous provision of ecosystem services. Specifically, Action 5 of Target 2 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". Thus, spatially-explicit mapping of ecosystem services and a comprehensive synthesis of ES information in the context of the underlying environmental and socio-economic conditions are required by policy makers to tackle future challenges.

Several European countries have either initiated or compiled (sub-)national ecosystem assessments (eight of which are reviewed in Schröter et al., 2016). These efforts range from the collection of suitable ES indicators in Germany (Albert et al., 2015; Rabe et al., 2016) and Switzerland (Staub et al., 2011), to the completion of full ecosystem assessments (e.g. UK NEA, 2011). These programs differ widely regarding the aims, political context, spectrum of methods and level of implementation (Schröter et al., 2016). Maes et al. (2016) developed a conceptual framework for ecosystem assessments in the EU to support future national mapping efforts and to allow comparability among member states. This framework proposes a typology of available ES indicators based on the *Common International Classification of Ecosystem Services* (CICES; Haines-Young and Potschin, 2013), while taking into account data availability at the European level and the ability to convey information to policy and decision makers.

(Sub-)national assessments, which are a time-consuming endeavour (e.g. the UK National Ecosystem Assessment involved more than 600 authors and took two years), should synthesise information on ES for decision makers (Maes et al., 2013). Analys-

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ing ecosystem service bundles (hereafter ESB), defined as "sets of services that appear repeatedly together" (Raudsepp-Hearne et al., 2010), is an efficient way to compile and convey such information. ESBs allow a systematic and synoptic description of landscapes based on the importance and co-occurrence of different ES. This provides insights regarding differences in ES provision and use across space (e.g. Turner et al., 2014; Queiroz et al., 2015) and time (Renard et al., 2015). Furthermore, the consideration of multiple ES is essential to obtain a greater understanding of how ES trade-offs and synergies (*sensu* Raudsepp-Hearne et al., 2010) may change within and between regions. However, ESB studies rarely include a thorough analysis of environmental and socio-economic covariates to understand how the composition of ESBs is linked to nature and society (but see Renard et al., 2015; Crouzat et al., 2015).

Given the current diversity of methods for analysing associations between ES (Mouchet et al., 2014), our goal here is to present a transferable and widely applicable blueprint for analysing ESBs at regional to national scales. The key component is the application of self-organizing maps (SOM, Skupin and Agarwal, 2008), an unsupervised clustering technique based on artificial neural networks, that was recently featured by Mouchet et al. (2014) as an efficient way to delineate ESBs. SOM reduce high-dimensional data by grouping observations based on their similarities while it preserves topological properties of input data (Skupin and Agarwal, 2008) and thus it is suitable for spatially-explicit mapping of co-occurring ES. The ability of SOM to visualize clustered patterns in complex data is widely acknowledged in environmental sciences, e.g. in studies of ecological communities (Giraudel and Lek, 2001), in water related applications (Kalteh et al., 2008) or in mapping of European and global land systems (Levers et al., 2015; Václavík et al., 2013).

Focusing on Germany as a case study, we propose a reproducible approach which integrates ESBs with socio-environmental conditions and can assist other EU member states in fulfilling the basic requests of the *EU Biodiversity strategy to 2020* (European Commission, 2011). This approach comprises a series of steps. First, we start with the collection and harmonization of spatial data on ecosystem service indicators as well as socio-environmental covariates. Second, we delineate ecosystem service bundles and socio-environmental clusters (SEC; see Section 2.5 for details) using the SOM method. Finally, we describe the relationship between the spatial configuration of ESBs and SECs based on an overlap analysis. To illustrate the main outcomes, we present spatially-explicit maps that highlight the regional patterns in ecosystem service provisioning and underlying socio-environmental gradients. This approach allows us to answer the following questions, relevant to science, policy and management, and partly raised also in recent ES studies (Bennett et al., 2009; Raudsepp-Hearne et al., 2010; Turner et al., 2014; Schmidt et al., 2016):

Q1 Which ecosystem services are most important for a specific region and form ecosystem service bundles? How are these bundles distributed in space?
Q2 Which regions provide a multitude of ecosystem services potentially indicating multifunctionality?
Q3 Which are the focus areas (hot spots) to be studied in more detail within a national ES assessment and to pinpoint future research and management questions?
Q4 How is the composition of existing ecosystem service bundles linked to social and environmental gradients?

2. Materials and methods

2.1. Study area

Germany, being the fourth largest country within the European Union by area (Eurostat, 2014), underwent far-reaching land-use changes after the Second World War. This process characterized by land-use intensification, further mechanisation and specialisation of agricultural systems together with industrial livestock farming and intensive grassland management (e.g. Antrop, 2005) changed the provisioning of and demand for various ES. These factors led to major trade-offs, e.g., agricultural production vs. water purification (Berka et al., 2001) or biodiversity conservation (Flynn et al., 2009). Forest areas, mainly located in Southwestern and Southern Germany at higher altitudes as well as Eastern Germany, account for 34% of the total land area. Cropland occupies 33% of the total land area, mainly located in Central and Northeastern Germany as well as in the lowlands of Southern Germany. Grasslands are mainly located in Northern and Northwestern Germany as well as at average heights in the hilly and mountainous regions and account for 23% of the total land area. Both cropland and grassland area are above the European average. Germany has a coast line with the Baltic Sea and the North Sea in the North whereby Mountainous regions characterize Southern Germany. Even though the German reunification took place more than 25 years ago, socio-economic differences between the eastern and western part are still apparent today (Damm et al., 2015). Due to the organization of farmers in agricultural cooperatives in former German Democratic Republic (GDR), differences in the current land-use can also be detected, e.g. leading to variations in average field sizes ranging from 55 to 232 ha in Western and Eastern Germany, respectively (Gurrath, 2011). The sovereignty of the 16 federal states poses large challenges regarding the collection and harmonization of spatial environmental data.

2.2. Ecosystem service indicators

Following the framework of Maes et al. (2016), who proposed 27 indicators for mapping 21 ES in terrestrial and freshwater ecosystems throughout Europe, we collected 12 indicators representative for eleven ES (see Table 1 and Appendix A.1). The main criteria for selecting ES indicators were also data availability and geographical coverage which in turn were strongly affected by the federal German system. Seven out of the eleven ES employed in our analysis have been identified as being of high importance for Germany (see Table A3 in Rabe et al., 2016). To ensure comparability with other ES studies in Germany (Albert et al., 2015; Rabe et al., 2016) and enhance reproducibility of our approach in other countries, we applied the hierarchical CICES system (Haines-Young and Potschin, 2013) as typology. The mapped indicators refer to ES potential, supply or demand depending on the specific ES (see Maes et al., 2016).

The indicators used here result either from primary data or from different types of models and refer to different spatial scales or units (e.g., districts, regular grids, river basins; see Table 1). To harmonize the various data sets, we resampled all indicators to a regular grid of 10 × 10 km using the standardized European equal-area reference system developed for statistical mapping (ERTS89). This reference grid, representing a compromise between the fine and coarse-scale data available, was also used to aggregate the analysed environmental and socio-economic covariates. To improve downscaling of district level data, we employed high resolution land-use data (GeoBasis-DE/BKG, 2010) and calculated the exact proportion of individual land-use categories for each reference grid cell. For example, we used the proportion of grassland per grid cell to spatially allocate estimates of the total number of livestock units per reference cell based on data about average numbers of livestock units per hectare available only at district level (see Appendix A.1). For data at finer resolution than 10 × 10 km, the average value per reference grid cell was calculated. As urban ecosystems and their ES have special characteristics and cannot be assessed easily with the same indicators as non-urban ecosys-

Table 1
Indicators used to assess supply/potential of or demand for ecosystem services using the CICES typology (version 4.3); scale, type and reference of input data are provided.

CICES Class v4.3	Short Name	Indicator (Unit)	Category	Scale	Data type	Availability of data	References
Provisioning services							
Cultivated crops	Crop production	Energy produced by main crops(GJ)	Supply	District	Primary data	Public access	Regional database (2014a,b,c); LFL (2013); Greef et al. (1993); GeoBasis-DE/BKG (2010)
Reared animals and their outputs	Livestock production	Number of livestock units (LU)	Supply	District	Primary data	Public access	Regional database (2014d); GeoBasis-DE/BKG (2010)
Surface water for drinking	Clean water	Nitrogen concentration in rivers(mg N/l)	Potential	River basin	Model	On request from authors	Bouraoui et al. (2000), Grizzetti et al. (2005), Grizzetti and Bouraoui (2006); Grizzetti and Bouraoui (2008)
Fibres and other materials from plants, algae and animals for direct use or processing	Wood production	Harvest likelihood combined with production statistics ($m^3/km^2/yr$)	Potential	1 km^2	Model	On request from authors	Verkerk et al. (2015)
Plant-based resources	Energy crops	Amount of methane provided by crops for biogas production (m^3 CH_4/yr)	Supply	District	Primary data	On request from governmental company	DBFZ (2011), FNR (2015); Rensberg et al. (2012)
Regulating/maintenance services							
Filtration/sequestration/storage/ accumulation by ecosystems	Nitrogen retention	Ability of rivers to remove nitrogen (% differences to concentration without nitrogen retention)	Supply	River basin	Model	On request from authors	Bouraoui et al. (2000), Grizzetti et al. (2005), Grizzetti and Bouraoui (2006); Grizzetti and Bouraoui (2008)
Mass stabilisation and control of erosion rates	Erosion control	Soil loss due to water erosion affected by land cover and agricultural management (100 kg/ha/yr)	Supply	1 km^2	Model	On request from governmental organization	Wurbs and Steininger (2011)
Flood protection	Flood regulation	Biophysical dependent flood regulation by catchments (0–1; low to high)	Supply	1 km^2	Model	On request from authors	Stürck et al. (2014)
Pollination and seed dispersal	Pollination potential	Habitat suitable for pollinators (% area)	Potential	1 km^2	Model	On request from authors	Schulp et al. (2014)
Cultural services							
Experiential use of plants, animals and land-/seascapes in different environmental settings (incl. physical aspects)	Distant recreation	Number of overnight stays (No./km^2)	Demand	District	Primary data	Public statistic	Regional database (2015)
	Water recreation	Lakes within 6 km radius of settlements (% area)	Potential	District	Primary data	On request from authors	Marzelli et al. (2014)
	Landscape recreation	Protected areas within 6 km radius of settlements (% area)	Potential	District	Primary data	On request from authors	Marzelli et al. (2014)

tems, the 76 largest cities in Germany (i.e., those with more than 100,000 inhabitants in 2013, covering an area of 11,825 km^2) were excluded from the analysis.

2.3. Analytical framework

The different steps undertaken in our approach are shown in Fig. 1, which summarizes the flow of data and results gained, highlighting the applicability of the approach for evaluating ESBs and associated SECs. ESBs and SECs in this context are patterns of co-occurring ES and socio-environmental covariates, respectively, identified using a self-organizing map clustering technique. These spatial clusters provide information regarding the dominance as well as deficiency of certain ES and underlying environmental or socio-economic covariates in specific regions, described in terms of their deviation from the national average. Spatial overlap analysis is used to identify the co-occurrence between ESBs and SECs to assess which socio-environmental conditions characterised and likely led to given ESB.

2.4. Ecosystem service bundles

To estimate and map the ESBs we implemented the SOM algorithm (package *kohonen*, Wehrens and Buydens, 2007; R version 3.0.2, R Development Core Team, 2013) on 12 ES indicators (see Table 1). At first ES indicators were standardised using z-score normalization to obtain zero mean and unit variance which removed the different units of the input data. This normalization allowed us to interpret the variable values of each cluster as deviation from the German national average represented by zero. These patterns of variable values are so-called ‘codebook vectors’ characterising each cluster (e.g. Václavík et al., 2013) and can be plotted as bar plots for visualisation purposes. In the second step SOM were parametrised by defining *a priori* the number of clusters typically organised in a 2-dimensional output plane (Levers et al., 2015, but see Giraudel and Lek, 2001). This step is crucial as selecting too many clusters may result in separation of relatively homogenous clusters, while selecting too few clusters may yield inhomogeneous clusters with high variability of the input data (Levers et al., 2015). We tested different numbers of clusters (from four to 30) in differently shaped output planes (e.g. 2 by 2 vs. 4 by 1) in two sensitivity analyses. One sensitivity analysis was based on the Davies–Bouldin index which calculates intra- and inter-cluster variability (Davies and Bouldin, 1979; Levers et al., 2015), whereas the other determined the mean distance of the classified grid cells to the codebook vectors of the cluster they belong to (Václavík et al., 2013). These sensitivity analyses revealed an optimum number of 8 clusters organized in a 2 by 4 hexagonal plane (see Fig. A.1 showing the outcomes of the analyses). In the third step, the actual SOM clusters were calculated iteratively, and each

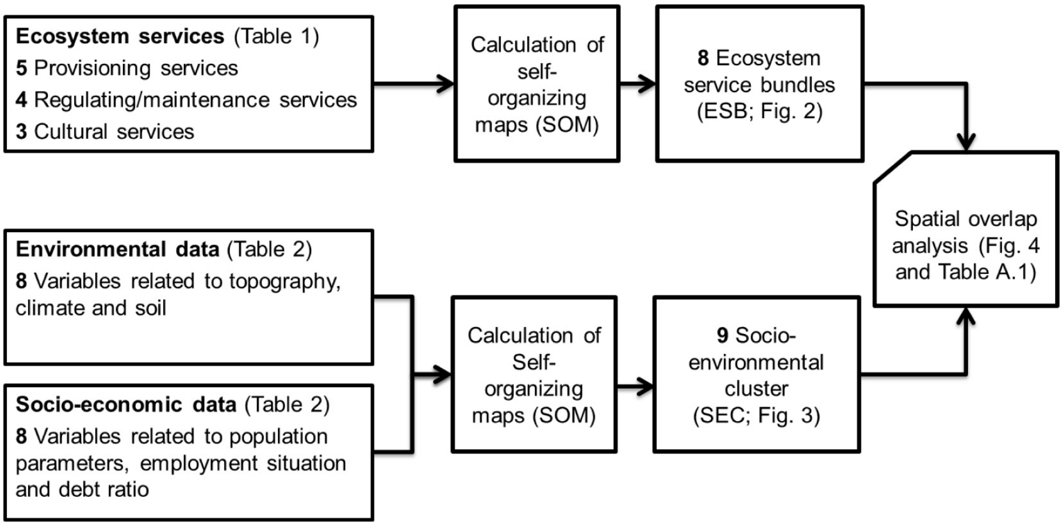

Fig. 1. Overview of the analytical framework, summary of the methods applied and reference to the results presented. The methodological procedure for analysing ESBs, SECs and their spatial overlap are described in detail in the next sections.

Table 2
Environmental and socio-economic variables used to calculate SECs; time (span), scale, and reference are provided.

Variable	Time (span)	Scale	References
Environmental variables			
Ruggedness	1950–2014	200 m	Geo-Basis-DE/BKG (2014)
Mean sunshine duration	1981–2010	1 km^2	DWD (2012)
Mean temperature vegetation period			
Mean precipitation vegetation period			
Groundwater level	2013	1:1.000.000	BGR (2013)
Usable field capacity root space			
Air capacity root space			
Ratio carbon/nitrogen			
Soil quality	2007	Municipalities	Roßberg et al. (2007)
Socio-economic variables			
Price of drinking water	2008–2011	Districts	Regional database (2016a)
Employee tertiary sector	2007–2011	Districts	Regional database (2016b)
Employee secondary sector			
Employee primary sector			
Ratio female/male	2007–2011	Districts	Regional database (2016c)
Population density			
Price building land	2007–2011	Districts	Regional database (2016d)
Unemployment rate	2007–2011	Districts	Regional database (2016e)
District debts	2007–2009	Districts	Regional database (2016f)

grid cell was assigned to the best matching cluster automatically which allowed mapping of the results for further analysis. We conducted 50 runs of the iterative SOM algorithm to discover the dominant cluster pattern and to determine pixel-level stability in cluster membership. After the dominant cluster pattern was determined, we further characterized the obtained ESBs. For this, we used the standardized codebook vectors to sum up the absolute values for all services belonging to the same CICES category (as defined by Haines-Young and Potschin, 2013) to determine how important the three categories of ES were for each ESB. This approach allowed us to classify the ESBs as provisioning, regulating/maintenance, cultural or mixed bundles.

2.5. Socio-environmental cluster

To estimate and map the SECs we implemented the SOM algorithm, following the same steps as described in Section 2.4., on 18 uncorrelated ($|r| < 0.7$, Dormann et al., 2013) environmental (related to topography, climate and soils) and socio-economic covariates (see Table 2). These variables are representative for the main environmental (Roßberg et al., 2007) and socio-economic gradients (Statistische Ämter des Bundes und der Länder, 2014) in Germany. Most of the data are updated regularly, which eases a potential future trend analysis. We did not include land use and land cover data as these data have been already used to calculate agricultural related ES indicators. The sensitivity analyses revealed an optimum number of 9 clusters organized in a 3 by 3 hexagonal plane (see Fig. A.1). We also used the codebook vectors to determine the relative importance of environmental and socio-economic variables in characterizing the identified SECs. To understand the link between the spatial configuration of the identified ESB and the underlying environmental and socio-economic conditions, we conducted a spatial overlap analysis using ArcGIS version 10.5 (ESRI, 2012). Subsequently we quantified the frequency of ESB co-occurrence with the nine SECs (see Levers et al., 2015) to indicate which variables are likely to account for the characteristics of certain ESB and vice versa.

3. Results

3.1. Spatial distribution and characteristics of ecosystem service bundles

Eight ESBs were detected composed of different contributions of provisioning, cultural and regulating/maintenance services (see Fig. 2b). Three of the bundles were mainly characterised by either very low or very high provisioning ES (ESB 1 to 3), another three mainly by cultural ES (ESB 4 to 6). The remaining two bundles were determined by regulating/maintenance services (ESB 7) or by an equal contribution of multiple ES (ESB 8) (see percentage values next to the bar plots in Fig. 2b and detailed information regarding ES provisioning per ESB provided in Table A.1). The cluster membership for all cells was highly stable among the 50 runs of the SOM algorithm ranging between 95% and 98% per ESB (see Table A.1 and maps of Fig. A.2 showing pixel-level stability throughout Germany).

ESB 1 (central loess plain around Harz mountain range and sub montane zones in Eastern and Southern Germany; Fig. 2a) is representative for the most important agricultural production areas in Germany. On the other hand, the potential for pollination and local water recreation is very low in this area (Fig. 2b, Table A.1). ESB 2 (north-western lowlands; Fig. 2a) is the hotspot for provisioning services and depicts an area specialized in the production of energy crops and in livestock farming but suffering from low water quality (Fig. 2b, Table A.1). ESB 3 (low mountain ranges; Fig. 2a) has a strong focus on wood production accompanied by a high potential for local landscape recreation. It thus belongs to the provisioning bundles while having a large share of cultural services (Fig. 2b, Table A.1).

Cultural services dominate ESB 4 (German Alps and the Black Forest; Fig. 2a) which represents the second most important area for distant recreation and has the highest potential for water recreation. Besides a strong focus on wood production, its potential for pollination is also high (Fig. 2b, Table A.1). ESB 5 (shoreline of the North Sea and the Baltic Sea; Fig. 2a) is the hotspot of the cultural bundles – or more precisely of distant recreation. Some scattered cells belonging to this bundle represent cells in the hinterland of bigger cities benefiting from their attractiveness for tourists (Fig. 2b, Table A.1). ESB 6 (Alpine foothills and the Bavarian low mountain ranges; Fig. 2a) characterizes the transition from the cultural to the regulating/maintenance bundles. While this area has a pronounced potential for pollination and is important for livestock farming, the potential for landscape recreation is limited and the estimated soil loss due to water erosion is high (Fig. 2b, Table A.1).

The main rivers in Germany (Rhine, Elbe, Weser and Oder) are represented by ESB 7 (Fig. 2a). Here, nitrogen retention and flood regulation are particularly important, making this the only bundle

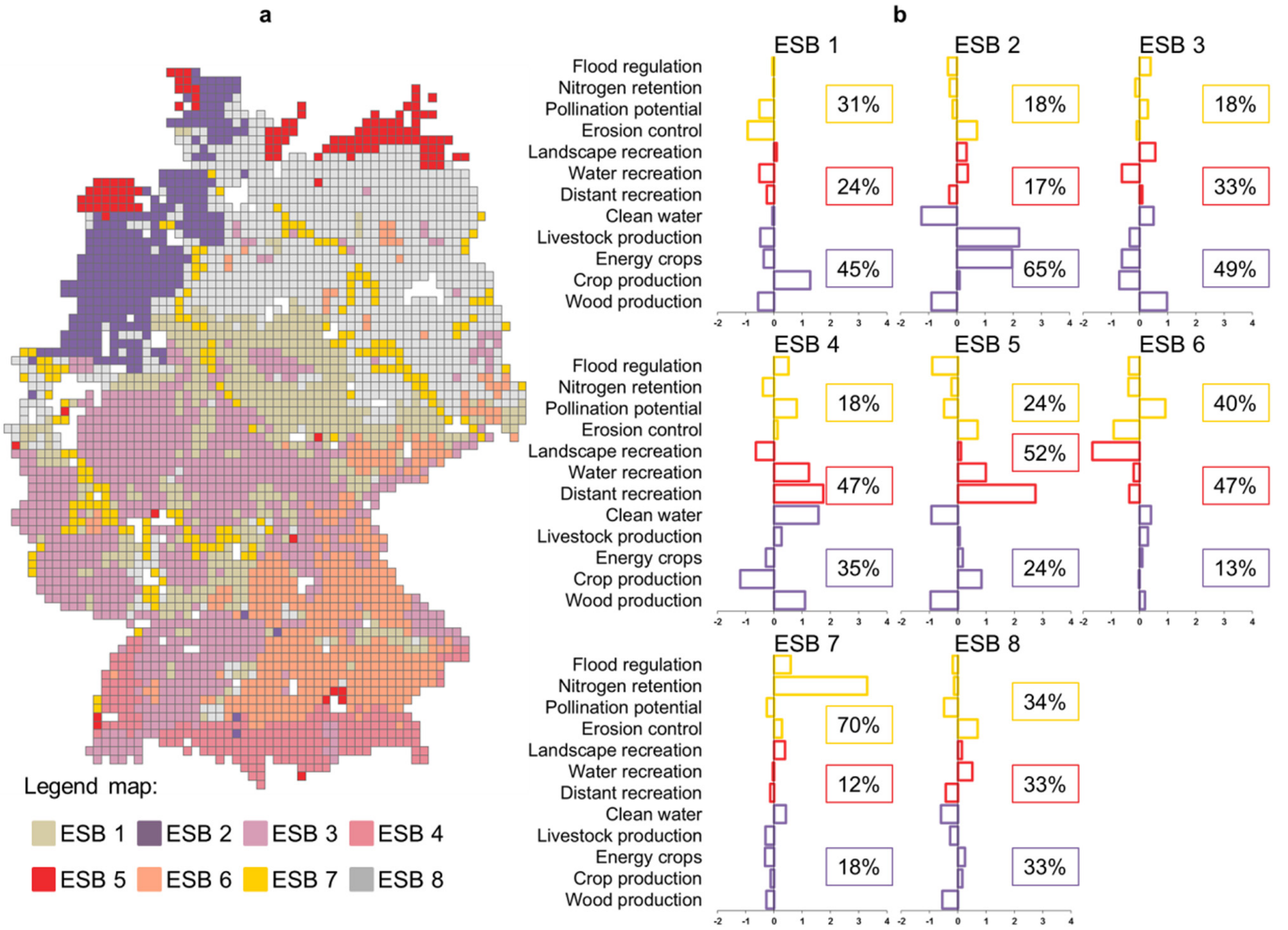

Fig. 2. Ecosystem service bundles (ESB) mapped in Germany (panel a). The bar plots (so called 'codebook vectors'; panel b) show the z-score normalized values of ES characterizing each ESB, with zero representing the national average. The relative contribution of the three categories of the Common International Classification of Ecosystem Services per ESB is indicated by the percentages next to the bar plots (purple: provisioning, red: cultural, yellow: regulating/maintenance). Percentage ratios per ESB are based on the total absolute values of the ES indicators (see Methods for further details).

dominated by regulating/maintenance services. These watersheds also provide high potential for landscape recreation (Fig. 2b, Table A.1). ESB 8 spreads over the north-eastern lowlands known for their heathlands as well as their lake scenery (Fig. 2a). This ESB has an equal share of all three ES sections; while energy crops are widely cultivated and the potential for water recreation is exceptional good, the potential for pollination and landscape recreation is intermediate (Fig. 2b, Table A.1).

3.2. Spatial distribution of environmental and socio-economic cluster

Nine socio-environmental clusters (SEC) were detected showing considerable spatial variation and heterogeneity throughout the study region (Fig. 3a). SECs dominated by environmental characteristics were mainly located in the north-western lowlands and the central part of Germany, whereas SECs dominated by socio-economic variables were found in the north-eastern lowlands and the highlands of Southern Germany. The northern lowlands can be characterized as a transition zone between these two sections (Fig. 3, Table A.1). The SOM algorithm, however, revealed less stable results regarding the spatial distribution of SECs compared to ESB assignment, with average pixel-level stability values per SEC between 58% and 97% (Table A.1, Fig. A.2).

3.3. Characterisation of ecosystem service bundles by socio-environmental covariates

Bundles being dominated by provisioning ES (i.e. ESB 1 to ESB 3; Fig. 2b) co-occurred spatially mainly with SECs determined by environmental variables (Fig. 4, Table A.1). ESB 2, being mostly dominated by provisioning services (Fig. 2b), overlapped nearly exclusively with environmental SECs (90%; Fig. 4, Table A.1). Various ESBs, however, related to two or even more dominant SECs. For ESB 4 to 6, which were classified as cultural bundles (Fig. 2b), the associated SECs belong to both the environmental and socio-economic space. ESB 4, which presented a high proportion of provisioning services, spatially overlapped to a wide extent with SEC 1, being mostly dominated by environmental variables (Fig. 4, Table A.1). The ESB with the highest importance of cultural services (i.e. ESB 5) covers mainly an area comprised by SECs with nearly equal importance of environmental and socio-economic variables (SEC 5 and 6; Fig. 4, Table A.1). ESB 6, having also a high importance of regulating/maintenance services, was mainly mapped in the area of the socio-economic SEC 7. ESB 7, which was classified into the regulating/maintenance section solely (Fig. 2a), spread over an area comprised by several SECs with a similar share of area belonging to both the environmental and socio-economic space (Fig. 4, Table A.1). The same was true for ESB 8, which showed a balanced share of services that could not have been clearly

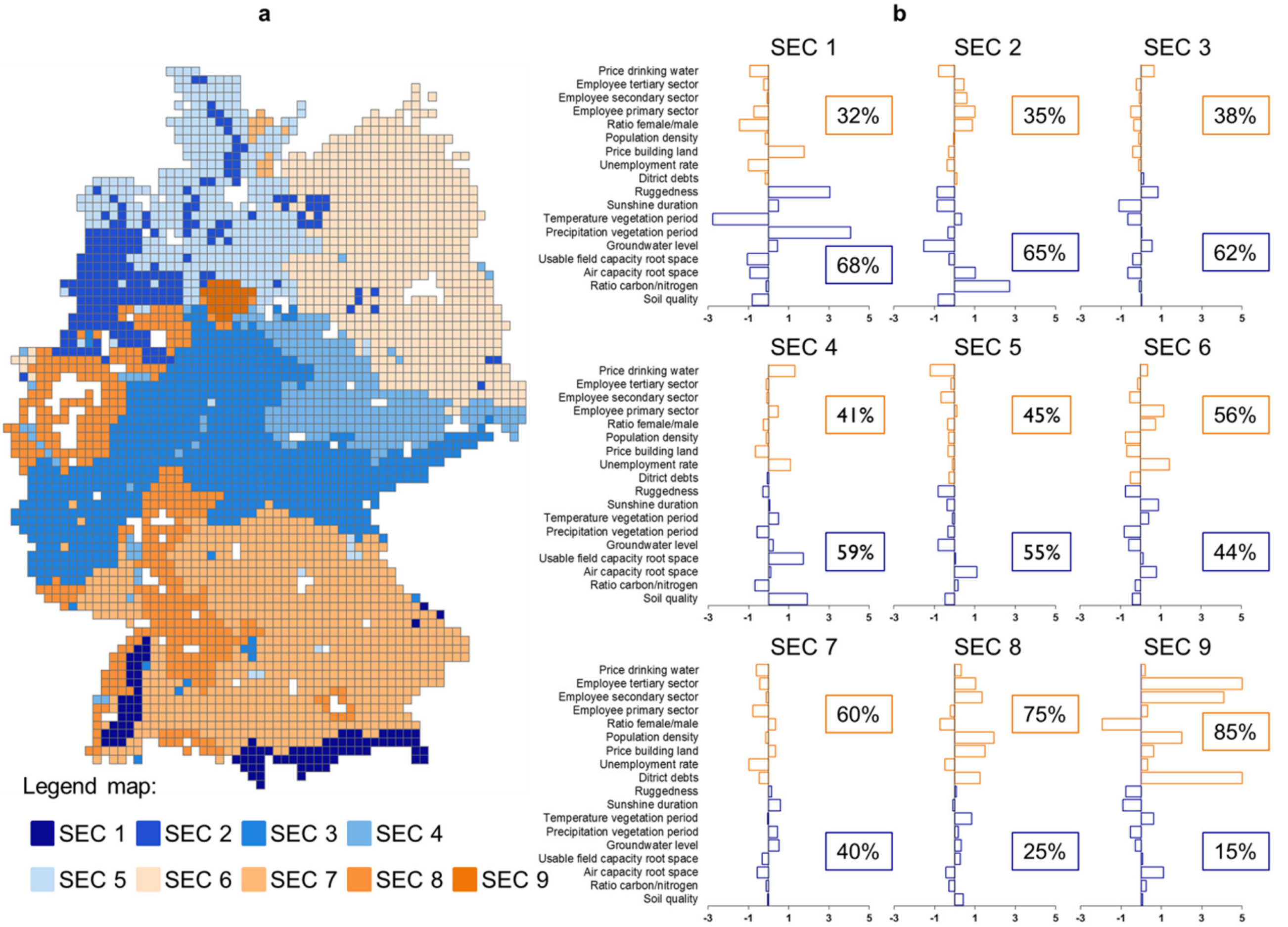

Fig. 3. Socio-environmental cluster (SEC) mapped in Germany (panel a). The bar plots (so called 'codebook vectors'; panel b) show the z-score normalized values of covariates characterizing each SEC, with zero representing the national average. SECs are dominated either by socio-economic (orange) or environmental (blue) covariates, with gradual colour transitions between both groups. The relative contribution of these groups per SEC is indicated by the percentage next to the bar plots. Percentage ratios per SEC are based on the total absolute values of the environmental and socio-economic covariates (see Methods for further details).

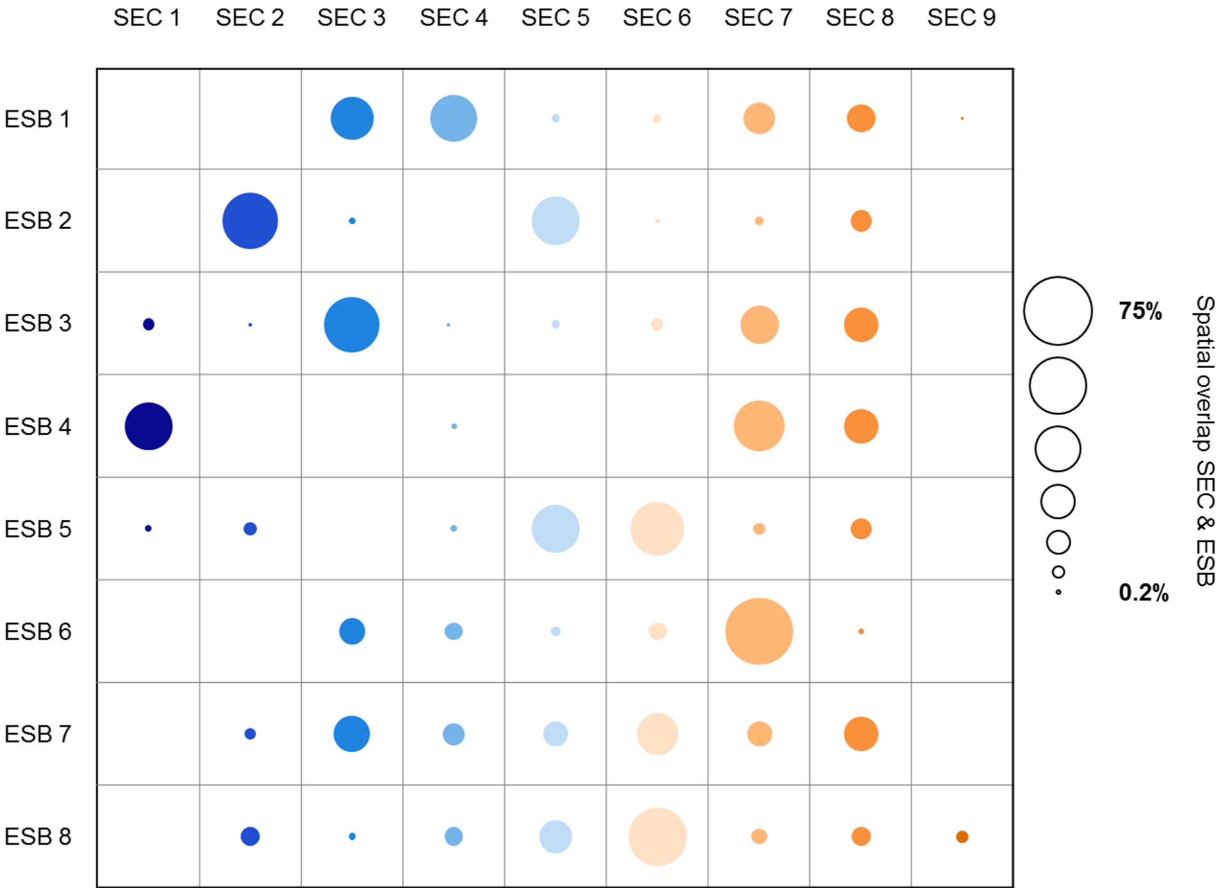

Fig. 4. Spatial overlap of each socio-environmental cluster (SEC) per ecosystem service bundles (ESB) in% of area. Rows sum up to 100% and circle sizes illustrate the extent of co-occurrence of the respected SEC and ESB. The spatial overlaps with provisioning bundles (ESB 1 – ESB 3) are shown in the upper part, the overlaps with cultural bundles (ESB 4 – ESB 6) in the middle part and the overlaps with regulating/maintenance ESB 7 and mixed ESB 8 at the bottom. The colours of the circles represent the dominance of environmental (blue) or socio-economic (orange) variables in characterising SECs, whereby colour intensity reflects the degree of dominance (dark: strong; light: weak).

assigned to one of the three CICES categories (Fig. 2a). The greatest overlap of ESB 8 was found with SEC 6, having a nearly equal importance of environmental and socio-economic variables (Fig. 4, Table A.1).

4. Discussion

4.1. General findings

This study offers the most comprehensive analysis of ES and their relation to socio-environmental variables in Germany to date. The implemented approach allowed us to answer the set of questions listed in the Introduction (see Section 1). Namely, it provides first insights into the issue of how the potential supply of considered ES is distributed and bundled at a national scale and illustrates which services are more/less abundant in certain regions (see Question 1; Fig. 2). We also found that our approach of identifying ESBs may indicate areas with a more multifunctional use of landscapes such as ESB 8 (see Question 2; Fig. 2b; see also Turner et al., 2014). Obviously, ES associations change among the ESBs and provide a valuable source of information to pinpoint future research and management questions (see Question 3; Fig. 2b and Table A.1). Exemplary findings from this study are trade-offs between intense livestock farming and water quality or between crop production and landscape-related recreation. By applying an overlap analysis with SECs we made a first step towards better understanding which environmental and socio-economic conditions determine and lead to a specific configuration of ESBs (Question 4; Fig. 4, Table A.1).

4.2. Spatial distribution and characteristics of ecosystem service bundles

Supporting the findings of recent studies on ESBs (e.g. Raudsepp-Hearne et al., 2010; Turner et al., 2014; Queiroz et al., 2015), we detected bundles mostly characterised by crop production, livestock farming and wood production (see Question 1; Fig.2a). This regional concentration of specific provisioning services likely reflects the ongoing specialization in land use and, especially, in agricultural production, which accelerated around 1950 (e.g. Antrop, 2005). A hot spot of tourism was found next to the shoreline in Northern Germany (Fig. 2), which agrees well with the results of a recent study in Denmark (Turner et al., 2014). The high values for recreation can be related to the scenic beauty of the sea. Moreover, large areas along the coastline in Germany have been designated as National Parks and other protected areas (BfN, 2015), providing infrastructure for nature appreciation and protection of resting places for migratory birds (Laursen et al., 2009). It is noteworthy that also the Alpine Mountains are attractive for distant recreation (Fig. 2b), especially for winter sports and hiking during summer. However, recreation appears to be a “ difficult-to-assess” ES with many different forms and manifestations (Plieninger et al., 2013), making it challenging to choose an appropriate indicator and to compare the identified ESBs with other studies.

Examining visually the ES associations within the individual ESBs (Fig. 2b) confirms the findings of Lee and Lautenbach (2016) who detected consistent patterns of ES trade-offs and synergies. In line with their results, we found a synergistic relationship, i.e. distinctively positive ES values above the national average, between different cultural services (ESB 5 and partly ESB 2 and 4; Fig. 2b) and between regulating/maintenance services (ESB 7, Fig. 2b). Trade-off dominated relationships, i.e. a combination of distinctively positive and negative ES values compared to the national average, between regulating/maintenance and provisioning services were typical for ESB 1 and 2 (Fig.2b). However, the type of ES associations was changing among the ESBs suggesting the need to further analyse the underlying mechanisms within a national assessment (see Question 3).

4.3. Relationship between ecosystem service bundles and socio-environmental covariates

An efficient and sustainable ES management requires detailed knowledge about drivers and underlying mechanisms of ES trade-offs and synergies (Bennett et al., 2009). Contrary to research focusing on pairwise ES associations, this issue is more difficult to tackle in ESB studies, mostly due to the high dimensionality of ES and covariates assessed. To our knowledge, only a few ESB studies have therefore considered socio-environmental covariates in more detail (e.g. Raudsepp-Hearne et al., 2010; Renard et al., 2015). This indicates a need for methodological refinement. The conducted overlap analysis is a promising approach in this direction but it is important to bear in mind that spatial co-occurrence does not necessarily indicate causal relationships (Mouchet et al., 2014)

We found that provisioning ESBs mainly overlapped with SECs determined by environmental variables (Fig. 4). This highlights the importance of local environmental conditions for provisioning ES, despite the substantial progress in agricultural practices in the last centuries which may have partly overcome the limitations of environmental conditions. Similarly, ESBs dominated by cultural ES (ESB 4 and 5), overlapped to a wide extent with two SECs determined largely by the environmental conditions but also the socio-economic conditions (Fig. 3b, Fig. 4, Table A.1). This can be explained by the fact that, in the present study, we focused on those types of recreation (i.e. distant recreation and potential for water related recreation; see Table 1) that require certain environmental settings (e.g., sunshine duration, temperature, terrain ruggedness) and that are, at the same time, affected by or affect the local society (e.g. in terms of unemployment rate, price of building land). The ESB 8, indicating multifunctional landscapes, overlapped mainly with the intermediate SEC 6 characterized by relatively equal levels of both socio-economic and environmental variables (see Section 3.2., Fig. 3b, Fig. 4). In this case, the absence of pronounced environmental gradients may have hindered a specialisation in certain provisioning services and in turn also prevent known trade-offs with regulating/maintenance services (e.g. Lee and Lautenbach, 2016).

4.4. Advantages of the presented approach

The applied SOM method, proposed by Mouchet et al. (2014) as an efficient way to delineate ESBs, has been rarely utilised in and ES context (but see Crouzat et al., 2015). We believe this method has several advantages as it combines the capacities of Principal Component Analysis (PCA) and K-means clustering (i.e. reduction of dimensionality and cluster analysis). It further adds a spatial component to the analysis by preserving topology of the input space and thus directly accounts for spatial autocorrelation commonly detected for ES (e.g. Raudsepp-Hearne et al., 2010; Turner et al., 2014). Furthermore, the obtained codebook vectors (Figs. 2b, 3b) effectively summarize the characteristics of the determined ESBs and SECs, which serve as a straightforward approach to visualise results (e.g. Václavík et al., 2013). As the SOM method can be applied at different spatial scales, ranging from global (Václavík et al., 2013) and continental scales (Levers et al., 2015) to the plot level (Park et al., 2003), this algorithm is also suitable for nationwide studies allowing a comparison of the results with other studies conducted at a regional scale (e.g. Raudsepp-Hearne et al., 2010; Queiroz et al., 2015). Other ESB analyses most often refer to administrative units (e.g. Renard et al., 2015) because available data are derived from official statistics or surveys and because political decisions are mostly steered at this scale. However, modelled ES results and most other environmental data are typically collected using a grid cell-based approach, which is typical also for biodiversity monitoring programs. Thus the use of administrative units is seriously hampering the understanding of connections and trade-offs between biodiversity and ES, which is also relevant for the EU Biodiversity Strategy (Maes et al., 2012). We therefore used the regular grid developed by the European Union for statistical mapping in ETRS89 format.

4.5. Data inputs

Identifying suitable indicators for mapping and evaluating ESBs is case- and study area-specific. For Europe, Maes et al. (2016) proposed 27 suitable indicators representative for terrestrial and freshwater ecosystems. However, not all of them must be of national importance for informing policy and nature conservation. For Germany, Rabe et al. (2016) identified 11 ES indicators as being highly important at a national level, from which we were able to use a subset of seven indicators in the present study due to data availability. We selected additional five ES indicators to provide a more comprehensive set of ESB indicators, which can be part of a monitoring system in the future, not only in Germany but also in other geographical and environmental settings. The data we employed were publicly available but we also used published results from other authors. Given their approval, these data can be used in related studies in other countries since they are available at the European scale (see Table 1). ES indicators derived from calculations based on public data and official statistics can very likely be reproduced for other study areas. A few indicators such as energy crops, which were in this study based on extensive surveys from a governmental company, are generally more difficult to obtain and will require case-specific solutions.

While we believe the chosen grid cell approach is highly valuable, some uncertainties remain in the downscaling process of the data preparation, which may consequently affect the credibility of input data (e.g. Barsugli et al., 2013). However, most of developed scaling techniques relate to climate variables (Hewitson and Crane, 1996) and less to the problem faced here, i.e. downscaling of relatively broad scale agricultural statistics to an intermediate scale of 100 km^2. As agricultural data are closely related to certain land-use classes, we decided to calculate the extent of each land-use class of interest per reference cell and to multiply this area with an average value referring to one hectare. In doing so, we depict changes in ES provisioning within the different districts. As we have no primary data for validation, it remains difficult to judge the reliability of this approach. Further uncertainties may arise when comparing water-related services and terrestrial services. The meaningful reference unit for the former is a watershed, which may not be suitable for terrestrial services, such as wood production.

Another important issue in ES studies is the mixing of the supply and demand sides of ES indicators (*sensu* Burkhard et al., 2012) because the results of the trade-off and synergy analysis may become diluted. However, this issue is generally less problematic in studies on ES co-occurrence than for more complex analyses of drivers/mechanisms and spatial optimization approaches (Cord et al. in review). Furthermore, most studies comprising an extensive set of ES have to rely on already existing data, making it difficult to address both the supply and demand aspect. Against this background, recent studies on indicator development differentiate between supply and demand (Albert et al., 2015; Rabe et al., 2016), thereby helping to identify and illustrate the data needs for monitoring of ES in the future.

5. Conclusion

This study presents a blueprint to assess ecosystem service bundles at a macroscale or at the national level which can be repeated in other EU member states to support reporting requirements for the *EU Biodiversity Strategy* and other initiatives. The proposed approach is versatile because it is reproducible in other geographical context, flexible in terms of data input and spatially-explicit, allowing to map ESBs at different spatial scales. By applying the proposed blueprint for Germany, we identified clear patterns of ecosystem service bundles at a national scale, similar to studies conducted at a regional scale (e.g. Raudsepp-Hearne et al., 2010; Queiroz et al., 2015). This was especially true for bundles mainly characterized by provisioning services, which reflects the ongoing specialization in land use and specifically in agricultural management practices. Furthermore, the coastline and the mountainous regions, in Northern and Southern Germany respectively, were especially appreciated for their recreational value, which is true for similar regions in other European countries, as shown by Turner et al. (2014). We also identified an area in north-eastern Germany, which had no clear specialization in provisioning, regulating/maintenance or cultural services, indicating a more multifunctional use of landscapes. Using this approach at a national level may help identify regional responsibilities for certain services as well as specific environmental issues (e.g. low water quality associated with high numbers of livestock; low potential for landscape related recreation but high values for crop production). This pinpoints future research areas that should assess potential causal relationships among ES that are important for landscape management. As a next step, we plan to integrate biodiversity indicators to better understand linkages between ES supply/potential and biodiversity patterns. Future research of ESBs should also address the link between the regional and national scale to identify scale dependent changes in ES associations.

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Appendix A. Supplementary data

Supplementary data associated with this article can be found, in the online version, at http://dx.doi.org/10.1016/j.ecoser.2017.08.007.

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Appendix 5

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Regional-scale effects override the influence of fine-scale landscape heterogeneity on rice arthropod communities

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ABSTRACT

Irrigated rice croplands are among the most biologically diverse agroecosystems globally; however, intensification and simplification of farmed areas into homogeneous monocultures can lead to biodiversity loss and a reduction of associated ecosystem services such as natural pest regulation. Understanding how landscape heterogeneity affects the diversity of arthropod communities is therefore crucial for the sustainable management of rice agroecosystems. Here, we examine the influence of fine-scale landscape heterogeneity and regional-scale effects on the arthropod communities of three rice-production regions in the Philippines. Our analysis of 213 arthropod morphospecies (37,339 individuals) collected using two sampling methods at 28 field sites indicated that the rice agroecosystems in each study region had unique arthropod assemblages, likely reflecting region-specific environmental and land-use conditions. For all sites together, we found no effect of fine-scale landscape context (classified as rather high or low heterogeneity sites) on assemblage structure (arthropod abundance, species richness or diversity). When assemblages were analyzed separately, significant effects of fine-scale landscape context were only detected in one region and for two functional groups (predators and detritivores). Elevation gradient, used as a proxy for regional-scale effects in the study regions, explained more than 60% of variance in assemblage structure. Total arthropod abundance and rarefied species richness were negatively related to elevation, suggesting that regional-scale effects rather than fine-scale landscape heterogeneity explained the composition of rice-arthropod communities in landscapes. To further disentangle the complex effects of broad-scale environmental drivers versus fine-scale landscape complexity on arthropod communities and biocontrol services, future research in rice agroecosystems should focus on a more detailed quantification of landscape heterogeneity and examine its effect at multiple spatial scales.

1. Introduction

Rice (*Oryza sativa* L.) is the main staple food for nearly half of the world's population (Zeigler and Barclay, 2008) and is among the most important cereal crops in the developing world (Seck et al., 2012). With the World's human population expected to reach 9.2 billion by 2050 (United Nations, 2013), the demand for rice continues to grow, exerting increasing pressure on rice production systems (Ericksen et al., 2009). Rice agroecosystems have been classified as human-made wetlands (Ramsar, 2010). Because of their alternate dry and wet conditions and their largely tropical distribution, rice fields have been associated with high biodiversity (Cohen et al., 1994; Settle et al., 1996). Rice production promotes complex landscape mosaics because contiguous dry land is often interspersed with the flooded rice fields. These landscapes can attract a wide range of aquatic animals and plants. For example, Schoenly et al. (1996) recorded more than 600 macroinvertebrate species in conventional-cropped fields in the Philippines, which surpasses that of most natural temperate systems (Pimentel et al., 1992).

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Such high levels of biodiversity support complex interactions among multiple organisms, which help suppress rice pests and diseases and thus enhance rice production via biological control (Altieri, 1999; Bottrell and Schoenly, 2012; Macfadyen et al., 2015). Although agroecosystems are designed and managed by man to provide provisioning ecosystem services such as food, forage and bioenergy (Kremen, 2005), they strongly depend on regulating ecosystem services such as pollination and biocontrol (Power, 2010). The latter is of particular importance in rice agroecosystems as pest damage is considered a major limiting factor (Pathak and Khan, 1994).

Agronomic intensification tends to reduce diversity in agroecosystems through the expansion of farmed land, the loss of field margin vegetation, and high intensity management on existing cropland (Gerstner et al., 2014; Robinson and Sutherland, 2002; Swift et al., 1996). This further leads to the simplification and homogenization of farmed areas, resulting in considerably fragmented semi-natural habitats (Robinson and Sutherland, 2002; Meehan et al., 2011) and a degradation of biodiversity and ecosystem services (Tscharntke et al., 2005). In most agroecosystems, monocultures are characterized by higher levels of pest damage and smaller populations of natural enemies (Power, 2010; Gardiner et al., 2009), whose abundance and diversity are negatively affected by the lack of potential food resources and habitats (Landis et al., 2000). Therefore, understanding the effects of landscape heterogeneity and other environmental drivers on the diversity of arthropod communities is crucial to sustainably manage rice production systems and the surrounding landscapes with a minimum harm to agro-biodiversity (Ericksen et al., 2009).

High landscape heterogeneity, i.e. the fine-scale composition and configuration of crop and non-crop areas, is generally associated with increases in natural enemy abundance and diversity (Thies and Tscharntke, 1999; Gardiner et al., 2009; Woltz et al., 2012). While the role of arthropod diversity in maintaining natural pest regulation is not yet universally accepted as a basic principle by farmers (Bianchi et al., 2006), the evidence that landscape heterogeneity improves biological control is mounting (Bianchi et al., 2006; Letourneau et al., 2009; Chaplin-Kramer et al., 2011; Settle et al., 1996). Complex landscapes with large amounts of semi-natural habitat may benefit arthropod communities by providing (i) refuge from agricultural disturbances (Coll 2009; Kleijn and Sutherland, 2003; Meek et al., 2002), (ii) alternative hosts and prey or nectar resources, which are essential for many insects (Bugg et al., 1998), and (iii) a moderate microclimate, which can promote the survival of, for example, parasitoids that experience shorter lifespans at temperature extremes (Dyer and Landis, 1996, 1997). Although the positive aspects of landscape heterogeneity have been explored across a range of cropping systems and study regions (O'Rourke, 2010; Chaplin-Kramer et al., 2011), little is known about their effects on arthropod communities in complex rice production systems. For example, Wilby et al. (2006) documented landscape impacts on the processes of community assembly in rice, largely through effects on abundance, but they found only weak and sometimes contradictory patterns concerning the impact of rice cover and landscape heterogeneity on arthropod diversity.

In addition to fine-scale landscape heterogeneity, rice arthropod communities are affected by climate, environmental conditions and other landscape and land use factors operating at a regional scale. Regional-scale drivers, such as elevation gradients, provide "natural experiments" for testing the distribution of insect biodiversity (Körner, 2007; Samways, 2007). Elevation is often used as a surrogate variable for investigating the influence of regional climate conditions (Sanders et al., 2003), because both temperature and precipitation are highly correlated with elevation gradients. Temperature, in particular, plays a major role in the life history processes of arthropods (Sinclair et al., 2003), as it affects, among others, body growth and morphology, the number of instars and generations produced per year and the length of the life cycle (Hodkinson, 2005). In rice agroecosystems, the abundance of arthropods have been shown to decrease with increasing elevation but no significant trends were observed for species richness or diversity (Schoenly et al., 1996, 1998).

Whilst much emphasis has been placed in the past on describing the rice arthropod community itself (Heong et al., 1991, 1992; Schoenly et al., 1996, 1998; Settle et al., 1996), few studies so far have investigated the potential effect of fine-scale landscape heterogeneity or regional-scale effects on these communities. In this study we examine whether fine-scale landscape heterogeneity is positively related to arthropod diversity, particularly the diversity of natural enemies, in tropical rice fields. To do this we examined arthropod community structure at sites with either fine-scale high or low landscape heterogeneity within a 100 m radius and along an elevation gradient in the Philippines. By including sites at different elevations, we could examine the relative contribution of regional-scale effects and fine-scale habitat heterogeneity in structuring the communities. Furthermore, we assessed the utility of two sampling methods for examining aspects of rice arthropod community ecology.

2. Material and methods

2.1. Study sites

The study was conducted in three areas of 15 × 15 km (henceforth 'region') located on the island of Luzon in the Philippines (Fig. 1). These were the focal sites of a larger research project on sustainable rice production (LEGATO: Settele et al., 2015). The first region (PH_1) was situated in Laguna Province, southern Luzon, with study sites ranging in elevation from 25 m to 290 m asl. In these hilly lowlands, irrigated rice is double cropped, such that a standing rice crop including a ratoon crops is present during most of the year. Narrow plains and lightly undulating hills characterize the terrain. There are no remaining natural forests in the region, but agro-forestry is dominated by coconut plantations and other fruit trees. The second region (PH_2) was located in the Nueva Ecija Province of Central Luzon, at an altitude ranging from 45 to 60 m asl. This typical lowland region is characterized by flat relief with large expanses of irrigated rice and only few semi-natural non-crop habitats. Rice is double cropped using comparably high levels of mechanization and agricultural inputs. The third region (PH_3) was located in the mountainous Ifugao Province, at an elevation ranging from 780 to 1300 m asl. The terrain is diverse and characterized by rice terraces that are believed to have existed for up to 2000 years. The region also includes large patches of primary and secondary forest habitats. Traditional rice varieties are cultivated with relatively low mechanization and few agricultural inputs, typically with one crop per year, see Klötzbucher et al. (2015) and Burkhard et al. (2015) for additional details of the study regions and sites.

To examine the influence of fine-scale landscape heterogeneity on arthropod community composition, five pairs of fields (i.e. 10 core sites) were selected within each region (Fig. 1b) according to the composition of the surrounding landscape, resulting in a total of 28 core sites (sampling could not be performed at two of the core sites in PH_2, because vegetables and not rice were grown at the time of sampling). The mean distance between two core sites within each pair was ~369 m and ranged from ~177 m to ~1192 m. The core sites being relatively close to each other, they primarily differed in fine-scale landscape heterogeneity within each region while other potential regional-scale effects were similar for each pair. For each site, landscape surface coverage and the proportion of rice fields within a 100 m radius were visually estimated by the same observer. Each pair of sites consisted of: (a) a rice field surrounded by high heterogeneity (i.e., the proportion of rice surrounding the core site was substantially lower than 50% with dominance of non-rice habitats including other crops, forests or settlements); (b) a rice field surrounded by low heterogeneity (i.e., more that 50% of the surface coverage consisted of rice fields and with little non-rice habitat). Selected within consistent frame conditions, we assume that the low and high fine-scale heterogeneity sites

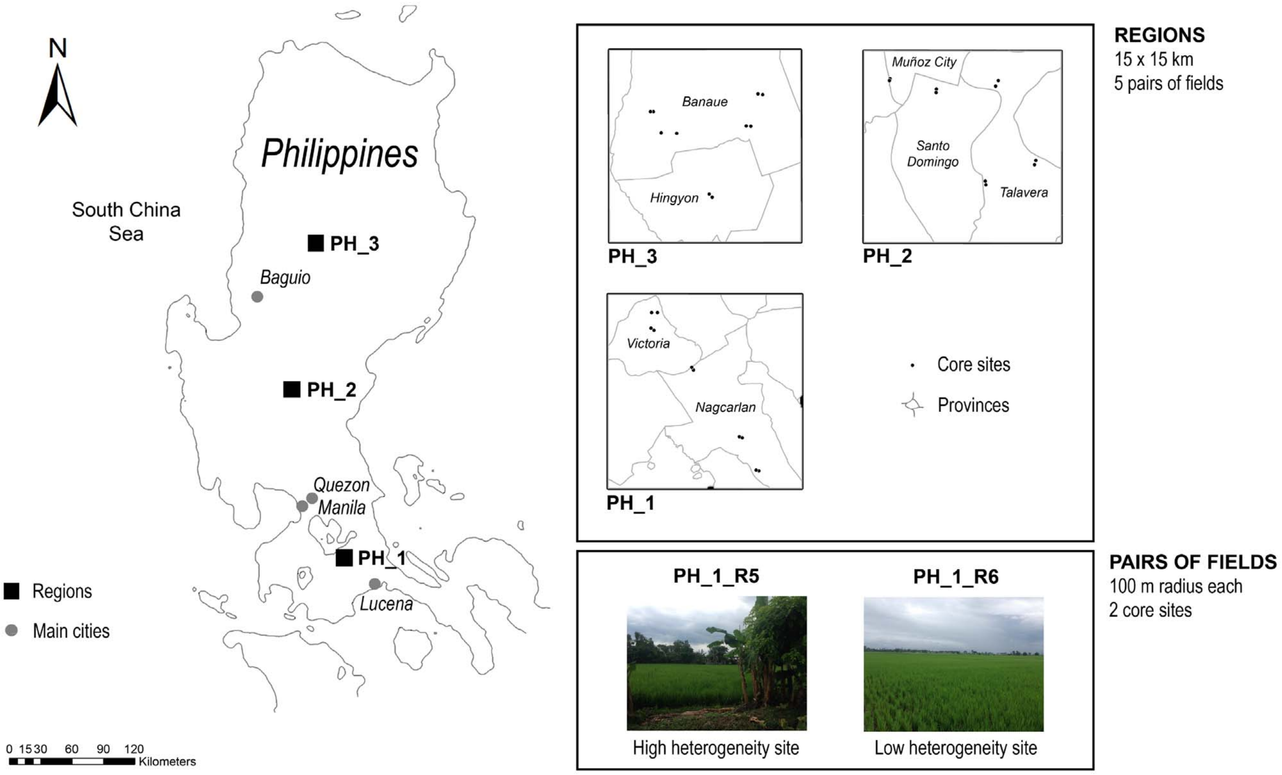

Fig. 1. Study area on the island of Luzon in the Philippines and locations of the 15 × 15 km regions in Laguna (PH_1), Nueva Ecija (PH_2) and Ifugao (PH_3). Locations of the core sites within each region and an example of high and low heterogeneity sites are presented.

allow a meaningful comparison of landscape heterogeneity and are also representative of the region in which they were sampled.

2.2. Arthropod sampling

Arthropods were sampled using a sweep net method and a vacuum (blow-vac) method similar to the one described by Arida and Heong (1992). For sweep netting, we used a standard canvas sweep net and performed thirty sweeps per sample at each core site while walking twice at a constant pace along a randomly established transect. For vacuum sampling, we used a custom built sampling enclosure of about 1 m side length that was placed over four rice hills to prevent any escape of mobile invertebrates. The suction time was prolonged until all organisms present inside the enclosure were collected by vacuum pressure into collection vials. Within each core site, five vacuum samples were taken at random locations.

Sampling for both methods was conducted in the center of each core rice field between 0700 and 1100 h, after morning dew had evaporated. In irrigated rice fields, the composition of the terrestrial arthropod communities changes with development of the rice crop and between cropping seasons (wet and dry seasons: Heong et al., 1991). Farmers in the Philippines usually produce two rice crops per year in the lowlands − one during the dry season (January to June) and one during the wet season (June to December) – but only one in the highlands (January–June). Therefore, to ensure consistency of sampling, the data collection was conducted during the dry season of 2013 in PH_1 and PH_2 and during the one-cropping season for 2014 in PH_3. In PH_2, vegetables were grown in the two core sites in 2013, thus limiting the pair of sites to four in this region. Sampling was performed at the maximum tillering stage of the rice plant (50 days after transplanting) because this stage is generally associated with a maximum abundance of arthropods (Wilby et al., 2006; Heong et al., 1991).

Sampled invertebrates were preserved in 70% ethanol. Most insects were identified using a binocular microscope to species level (or morphospecies level when species level was not possible) based on Barrion and Litsinger (1994); however, dipterans and collembolans, as well as arachnids were only identified to family level due to the morphological similarity at the pre-adult stages and the quality of the samples. In addition, the arthropods were grouped into functional guilds as follows: detritivores/tourists, invertebrate predators, parasitoids and herbivores. The "detritivores/tourists" guild is composed of detritivores and non-predatory species which have no direct association with the rice plant but which may be attracted to surrounding habitats (Moran and Southwood, 1982).

2.3. Statistical analyses

2.3.1. Characterization of the arthropod community

We characterized arthropod community structure as determined for each sampling method in each core site by calculating the abundance of all species, species richness (S) and the Shannon-Wiener index of species diversity (H'). To measure the differences in species structure among study sites, we performed non-metric multidimensional scaling (NMDS) ordinations after computation of a Bray-Curtis dissimilarity matrix based on arthropod abundances. The arthropod mean abundance data were square-root transformed prior to analyses, in order to reduce the influence of the most abundant species. As an additional test, we performed Ward's hierarchical cluster analysis of the Bray-Curtis dissimilarity matrix. Ward's algorithm is based on minimizing variances in hierarchically identified assemblages and performs well with aggregated data, for which the Bray-Curtis measure is generally recommended (Singh et al., 2010). The significance of the differences between arthropod assemblages derived from the Bray-Curtis matrix was assessed with a perMANOVA test. We also used a Mantel's test of spatial autocorrelation (based on a geographical distance matrix) to examine spatial dependence between study sites. Finally, we calculated

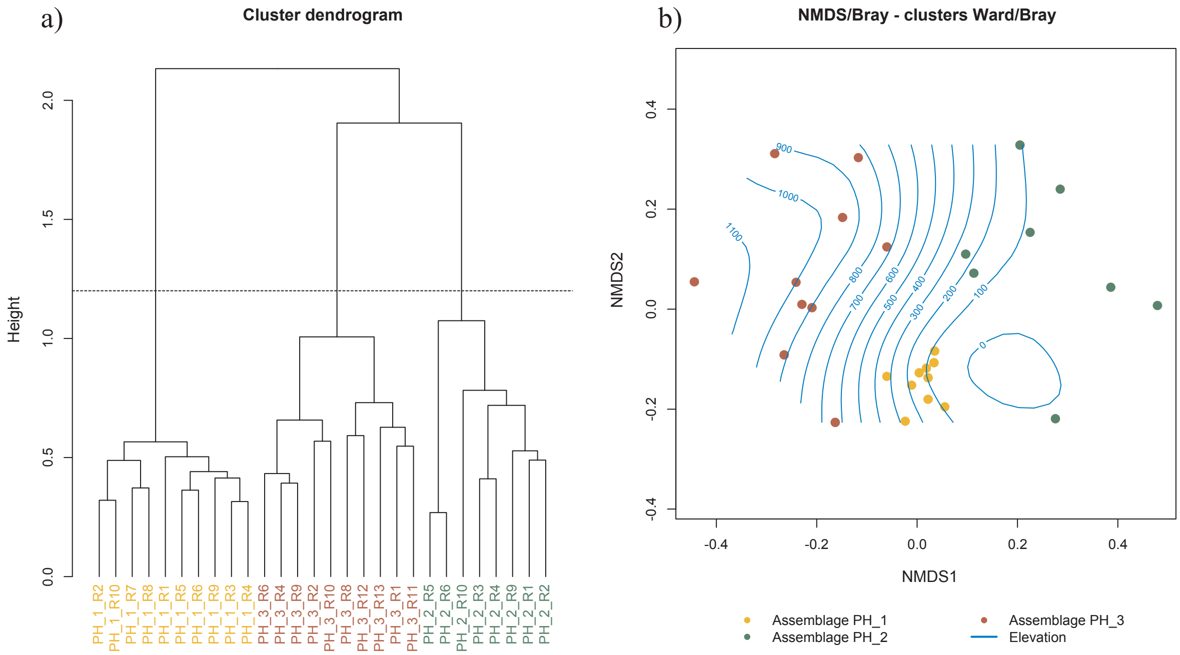

Fig. 2. (a) Ward's hierarchical cluster analysis based on Bray-Curtis dissimilarity matrix using square-root transformed arthropod mean abundance data of 28 core sites (data shown for the blow-vac samples). The cluster analysis identified three distinct assemblages (distinguished by color), each associated with one region. Core sites are abbreviated using the following nomenclature: PH represents the region; R represents the core site (i.e. PH_1_R2: Core site number 2 located in the region PH_1). (b) Non-metric multidimensional scaling (NMDS) analysis of the Bray-Curtis dissimilarity matrix (data shown for the blow-vac samples). The distance between sites indicates similarity of the arthropod community—the closer, the more similar. The variable that best explained the assemblage structure (i.e. elevation) is shown as surface fitting.

the relative contributions of each species to the similarities within each assemblage using a SIMPER analysis, which examines the percentage contribution each species makes to the similarity within and dissimilarity between assemblages (Clarke et al., 1993).

In order to determine if the sampling method had an effect on the identified arthropod composition, we used a Mantel's test to examine the concordance between dissimilarity matrices constructed using data collected by each sampling method. In addition, we compared the total mean abundance (square-root transformed) of the 20 most common species (representative of each order) sampled by each sampling method using a one-way analysis of variance (ANOVA). We also used an unpaired *t*-test to compare rarefied species richness across all regions between the two sampling methods. The rarefaction method was used here as it standardizes the measure of species richness, accounting for potential bias from different sampling efforts or other factors that may lead to large differences in the number of collected individuals among samples (Gotelli and Colwell, 2010).

2.3.2. Regional-scale effects and fine-scale landscape heterogeneity

In addition to distinguishing the two levels of landscape heterogeneity at sampling sites, we examined the effects of three basic environmental variables that are typical drivers of species distributions and community composition: elevation, mean annual temperature and mean annual rainfall (Atauri and de Lucio, 2001; Moreno-Rueda and Pizarro, 2007). The mean annual temperature and rainfall were both accessed from the CliMond archive at a resolution of 90 m (Kriticos et al., 2012). Elevation was obtained from the Advanced Spaceborne Thermal Emission and Reflection Radiometer (ASTER) Global Digital Elevation Model (GDEM) v2 at a 30 m resolution (https://lpdaac.usgs.gov/). As elevation and climate conditions are often closely related, we used Pearson's correlation coefficients to test for multicollinearity among environmental variables (Appendix A in the Supplementary material). As their variability was high among regions but low within regions, these predictors can be potentially confounded with other factors specific to regions PH_1, PH_2 and PH_3 such as environmental variables or larger-scale landscape structure.

To examine the influence of regional effects on the arthropod assemblages derived from the Bray-Curtis dissimilarity matrix, we used the *envfit* function from the vegan package (R Core Team, 2016). This function calculates the goodness of fit statistics provided by the squared correlation coefficient as a measure of separation among the different levels of the variables. The significant factor with the highest fit was then plotted on the MDS (Oksanen et al., 2016).

We also examined the impact of regional-scale effects and fine-scale landscape heterogeneity on species abundance, richness and diversity. First, we assessed the variable effects on the total mean abundance (square-root transformed), total rarefied species richness and total species diversity for all samples across all study regions using a one-way ANOVA. As an alternative, we tested the same variables with a linear mixed effect model using 'region' as a random effect. Second, we repeated the same analysis for the mean abundance (log transformed) of the morphospecies, which contributed the most to the similarities within each assemblage. Third, separately for each identified assemblage (PH_1–PH_3), we compared the abundance, richness and diversity measures between core sites with high and low levels of fine-scale landscape heterogeneity using a Student's *t*-test. We performed this additional analysis separately for each assemblage, in order to avoid the potential effect of region and account for the lack of spatial independence.

Then we provided the same comparison between sites with high and low levels of fine-scale landscape heterogeneity for both the functional groups in each assemblage and for the morphospecies which contributed the most to the similarities within each arthropod assemblage using a Student's *t*-test. Prior to statistical tests, we tested the normality of our data using the Shapiro-Wilk normality test. In the case of non-normal distributions, we used the Mann-Whitney tests instead of the *t*-tests. All statistical analyses were conducted in R version 3.1.1 (R Core Team, 2016).

3. Results

3.1. Characterization of the arthropod community

We recorded a total of 37,339 individuals representing 213 different arthropod morphospecies across the three different regions (Appendix B Supplementary material). The overall mean abundance was 69.8 (± 8.6), mean species richness was 14 (± 1.6) and mean species diversity was 3 (± 0.1) per core site for the sweep-net samples. Estimates of species diversity were similar between sampling methods; however, the estimated mean abundance (38.6 ± 3.7) and species richness (8.7) per core site was lower from the blow-vac samples.

Using the NMDS and Ward's cluster analysis for the arthropod community collected with the blow-vac sampling method, we identified three significantly different assemblages (perMANOVA, $R = 0.35$, $P = 0.001$), representing the three study regions PH_1, PH_2 and PH_3 (Fig. 2). An additional significant assemblage (PH_3b) was identified in the highland region when the analyses were applied to the sweep-net samples (Appendix C Supplementary material). In addition, significant spatial autocorrelation was observed among the core sites, as showed by a strong correlation between the dissimilarity matrix and a matrix of geographic distances between individual sampling plots (Mantel's $R = 0.41$, $P = 0.001$).

Located in the hilly Laguna Province, the assemblage PH_1 was the most homogeneous (average intra-group similarity: 58%) and its mean abundance (59.3 ± 2.8), species richness (17.3 ± 0.8) and species diversity (3.59 ± 0.05) were higher than the overall mean values across all regions. The arthropod communities located in PH_1 were characterized by a high abundance of detritivores/tourists such as chironomids, collembolans and other dipterans (~28% of the overall contribution; Fig. 3). The two main planthopper species, the brown planthopper, *Nilaparvata lugens,* and the whitebacked planthopper, *Sogatella furcifera,* were equally abundant. The predators were mostly represented by dwarf spiders (Linyphiidae) and wolf spiders (Lycosidae) (11% of the contribution). Based on their low intra-group similarity, both assemblages PH_2 and PH_3 (39% and 38%, respectively) were more heterogeneous than the assemblage PH_1. High abundances of lady beetles of the genus *Micraspis* and dwarf spiders were recorded in PH_2 (~22% contribution). While *N. lugens* contributed ~29% to the whole PH_2 assemblage, *S. furcifera* contributed less than 1% of the assemblage. On the other hand, in the PH_3 region, *S. furcifera* contributed ~19% to the assemblage, as opposed to *N. lugens* with less than 1%. The predatory mirid bug *Cyrtorhinus lividipennis* was collected in relatively high numbers at all sites in PH_3 (Fig. 3).

Sogatella furcifera and chironomids were the most abundant arthropods collected in the sweep nets (~50% of the total abundance), while *N. lugens*, *S. furcifera* and chironomids were most abundant in the blow-vac samples (more than 30% of the total abundance). In addition, *N. lugens*, *S. furcifera*, chironomids, *Tetragnatha* spp. (Tetragnathadiae), *Microvelia atrolineata*, dwarf spiders, wolf spiders, and collembolans (Isotomidae) were the most widely distributed arthropods according to blow-vac samples (present at more than 80% of core sites). *Nilaparvata lugens*, *Tetragnatha* spp., *Aranaea* spp. (Aranaeidae), chironomids, dipterans (other than chironomids) and *Micraspis* spp. were the most widely distributed species according to the sweep net samples (present in more than 80% of core sites). Sampling method had a significant effect on the relative abundances of most morphospecies (Fig. 4). When comparing rarefied species richness for the populations sampled by blow-vac and sweep net, we found a statistical difference for the region PH_1 ($t = -3.635$, $P = 0.003$) and PH_3 ($t = -8.644$, $P < 0.001$) but no difference for PH_2 ($t = -1.745$, $P > 0.05$). Despite these differences in detected abundance and rarefied species richness, the results of the Mantel test showed a significant concordance between the blow-vac and sweep net sampling methods (Mantel's $R = 0.56$; $P = 0.001$), indicating a similarity of the overall species composition for both sampling methods.

3.2. Regional-scale effects and fine-scale landscape heterogeneity

The pairwise Pearson's correlation tests between temperature, precipitation and elevation revealed that all variables were highly collinear ($|r| > 0.7$, $P < 0.05$). We therefore used only elevation in further analyses as a proxy for overall regional-scale effects in the study regions (i.e. other climatic, environmental and broad-scale landscape conditions).

For both dissimilarity matrices based on the two sampling methods, we found no effect of fine-scale landscape heterogeneity on the assemblage structure ($P > 0.05$). In contrast, elevation explained 65% of variance in the blow-vac samples and 68% of variance in the sweep net samples ($P < 0.001$). An elevation gradient fitted on the NMDS plot is shown in Fig. 2b for the blow-vac community and in Appendix C.2 Supplementary material for the sweep net community.

We also found no effect of fine-scale landscape heterogeneity on the total mean abundance, total species richness or total species diversity of the arthropod communities across all study sites. However, both the total mean abundance and total species richness of the communities were significantly negatively correlated with elevation ($F = 6.206$, $P < 0.05$ and $F = 9.175$, $P < 0.01$, respectively). When 'region' was included as a random effect, it substituted the influence of elevation (the range of elevation differed greatly among regions, while being lower within each region) but provided the same results regarding the effects of fine-scale landscape heterogeneity. We found no effect of landscape heterogeneity at this scale on those morphospecies that contributed the most to each assemblage across all study sites. However, we found multiple effects of elevation on the majority of morphospecies examined based on both the blow-vac and sweep net samples. Whereas most of the responses were negatively correlated with elevation, we found a positive correlation with elevation for the abundances of *S. furcifera* and *C. lividipennis* ($F = 5.789$, $P < 0.03$ and $F = 4.988$, $P < 0.02$ respectively) (Appendix D Supplementary material).

Comparing sites with high and low heterogeneity separately for each identified assemblage, we found significant differences only for abundance ($t = 2.814$, $P < 0.05$) and species richness ($t = -3.225$, $P < 0.02$) in PH_1 for samples collected with the blow-vac method (Fig. 5). In all other cases no significant differences were observed. Similarly, our results showed a significant effect of fine-scale landscape heterogeneity on only a few functional groups. For the blow-vac method, we found significant differences between high and low heterogeneity sites only for the abundance of detritivores and predators in PH_1 ($t = 3.149$, $P < 0.05$ and $t = 2.503$, $P < 0.05$, respectively) (Fig. 6), and the diversity of herbivores in PH_3 ($t = 2.449$, $P < 0.05$) (Appendix E Supplementary material). For the sweep net method, only the diversity of predators was affected by fine-scale landscape heterogeneity in PH_1 ($t = -2.571$, $P < 0.05$) (Appendix F Supplementary material). Furthermore, we found a significant effect of landscape heterogeneity at this scale only on two morphospecies (out of a total of 16) for the blow-vac community. In PH_1, the parasitoid *Oligosita* spp. was positively correlated with fine-scale landscape heterogeneity ($t = 0.345$, $P < 0.03$), while the aquatic predator *M. atrolineata* was negatively correlated with fine-scale landscape heterogeneity ($W = 16$, $P < 0.02$).

4. Discussion

We recorded a total of 213 morphospecies across the three regions, which correspond well with the number of species documented by Barrion et al. (1994) (240 species) and by Heong et al. (1991) (212 species). In Barrion et al. (1994), Los Baños (Laguna Province) showed the highest diversity of arthropods ($H' = 12.75$), while Banaue (Ifugao Prov.) had a lower diversity ($H' = 5.70$) and Cabanatuan (a city located in Nueva Ecija Prov.) exhibited the lowest diversity ($H' = 4.70$). Our results corroborate these findings, with PH_1 accounting for the highest

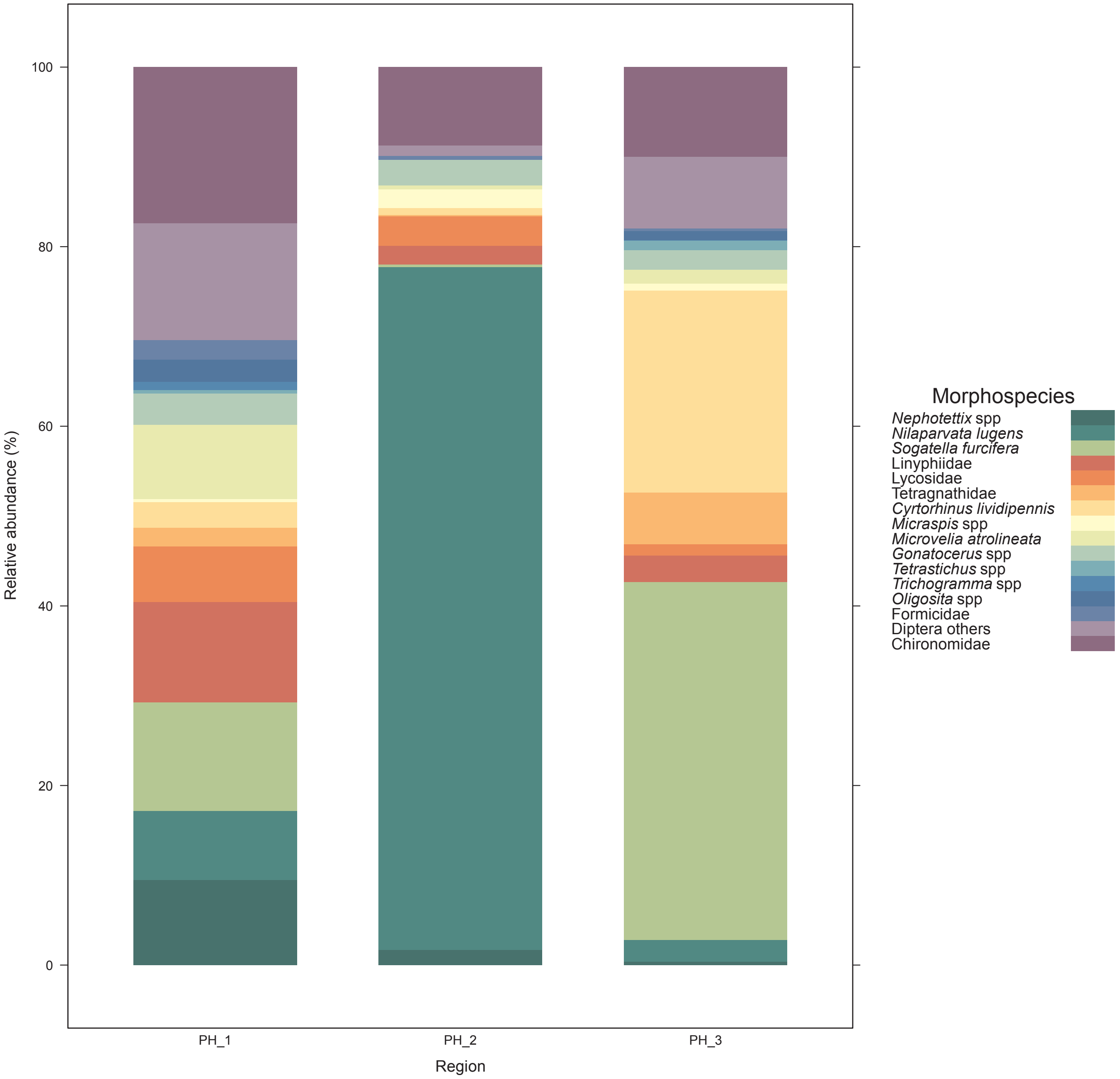

Fig. 3. Relative abundances of 16 morphospecies (calculated by SIMPER analysis) that contributed the most to the similarities within each arthropod assemblage identified based on Bray-Curtis dissimilarity matrix (data shown for the blow-vac samples).

species diversity, followed by PH_3 and PH_2. Our results showing that assemblages PH_3 and PH_2 are the most dissimilar (75.9% based on NMDS) also corroborate with Schoenly et al. (1996) who indicated that rice communities in Banaue and Cabanatuan were the least taxonomically similar (25%).

Although most of the common arthropod species were present in all three regions, the community structure differed from one region to another, resulting in three distinct assemblages. The positive spatial autocorrelation identified among core sites further supports this observation, showing that samples collected from nearby locations were also compositionally more similar than samples from locations further apart. The assemblage located in PH_1 included a higher number of species, a higher relative abundance and higher species diversity of the rice arthropods than the assemblages in regions PH_2 and PH_3, in addition to being more homogeneous than the other two sites. The PH_1 assemblage had also a relatively high number of detritivores that can potentially boost the abundance of generalist predators, which use detritivores as an alternative prey and may contribute to the relatively high resilience of irrigated rice systems (Settle et al., 1996). The high number of detritivores likely supported high numbers of two generalist spider families, Linyphidae and Lycosidae, as found in the Laguna region. The most common species of these two families are the lycosid *Pardosa pseudoannulata* and the linyphiid *Atypena formosana* (Barrion and Litsinger 1984; Kenmore et al., 1984; Sigsgaard 2000), which are important regulators of rice herbivores (Reddy and Heong, 1991). This was also reflected in our results, as *N. lugens*, *S. furcifera* and the green leafhopper *Nephotettix* spp. were the three main rice herbivores found in similar numbers across the PH_1 assemblage.

The assemblage PH_2 of Nueva Ecija had the lowest abundance, species richness and diversity of arthropods and had higher evenness than the other two assemblages, as is expected in intensive monoculture systems. *Nilaparvata lugens* was the dominant herbivore in PH_2, contributing to nearly one third of the total assemblage, while *S. furcifera* and *Nephotettix* spp. were largely absent. However, low numbers of predators and parasitoids were observed, likely due to the low quality of potential habitats caused by the high proportion of rice monocultures

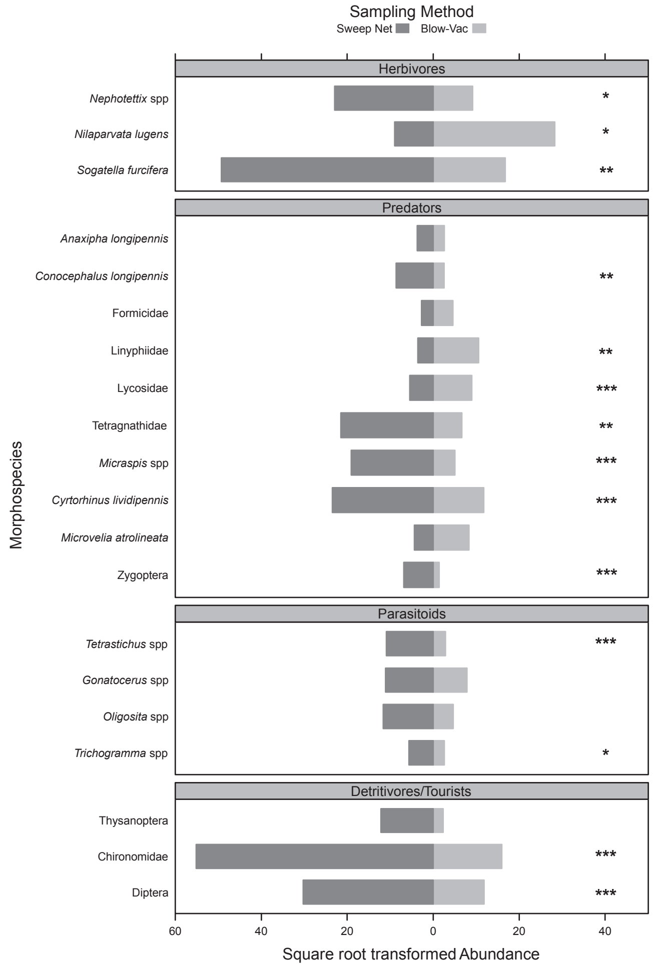

Fig. 4. Comparison of the mean abundance of the 20 most common morphospecies collected with blow-vac and sweep net. The list of morphospecies is grouped into four functional groups (from top to bottom: Herbivores, Predators, Parasitoids, and Detritivores/Tourists). Significant differences between sampling methods are indicated by asterisks located next to the bar plots (* $P \leq 0.05$; ** $P \leq 0.01$; *** $P \leq 0.001$).

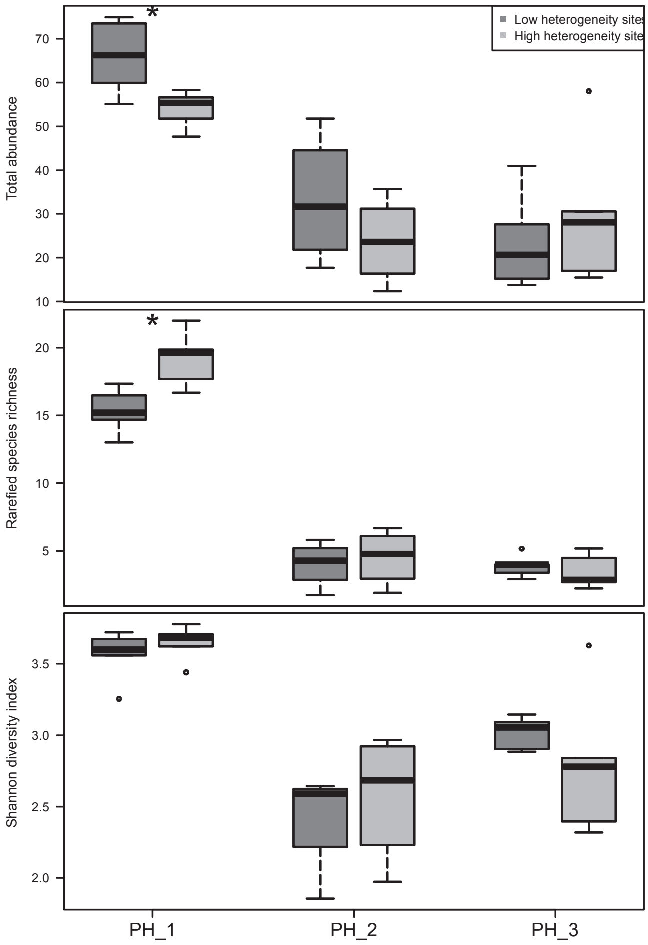

Fig. 5. Box-plots of the total mean abundance, rarefied species richness and species diversity (Shannon diversity index) of arthropods in sites with high (dark grey) and low (light grey) levels of fine-scale landscape heterogeneity (data shown for the blow-vac samples). Boxes show the median, 25th and 75th percentiles, maximum and minimum observations. Significant differences ($P < 0.05$) are indicated by asterisks.

in the region. In addition, *N. lugens* populations are known to increase drastically when main predators are removed (Kenmore et al., 1984). Modern rice varieties that are often accompanied by high levels of mechanization and chemical inputs (Burkhard et al., 2015) may also explain the disrupted assemblage structure in this region.

In the mountainous region of PH_3 Ifugao, *S. furcifera* was by far the most dominant herbivore species, representing nearly 20% of the total assemblage, whereas *N. lugens* contributed only 1%. The population of both herbivores in PH_3 was likely regulated by a combination of various predators such as *P. pseudoannulata*, *A. formosana*, *Tetragnatha* spp. and *C. lividipennis* (Barrion and Litsinger, 1984). The predatory bug *C. lividipennis* is a major predator of delphacids that consumes planthopper eggs and nymphs (Sigsgaard, 2007) and can consume over seven *N. lugens* nymphs daily (Reyes and Gabriel, 1975). The high numbers of *C. lividipennis* in PH_3 can be explained by the overwhelming presence of *S. furcifera* nymphs collected in the samples (~70% of nymphs collected).

Our results did not confirm the hypothesis that landscape heterogeneity within 100 m of sampling locations has a positive effect on the arthropod community. We found no effect of fine-scale landscape heterogeneity on assemblage structure and no differences in arthropod relative abundances, species richness or diversity between sites with a high and low level of landscape heterogeneity. Even when examining each identified assemblage separately, we found significant effects only in PH_1. Similarly, only one parasitoid and one predator out of the 16 morphospecies involved in the analyses, responded to landscape heterogeneity at this scale. In agreement with other studies of arthropods in agroecosystems (Altieri and Letourneau 1982; Weibull et al., 2003; Wilby et al., 2006), the locations with higher landscape heterogeneity in PH_1 had higher species richness. However, the lower total abundance and lower abundance of both predators and detritivores in PH_1 suggest that the increased species richness observed in more heterogeneous sites may be compensated by lower abundances, especially in these two guilds. For herbivores, we observed greater species diversity in the more heterogeneous sites of PH_3, but the predator group was neither more abundant nor diverse and therefore we cannot make any conclusion about the effect of landscape heterogeneity at this scale on natural pest control in our study regions.

These complex but largely inconclusive results regarding landscape heterogeneity may have several explanations. First, regional-scale effects, including effects of elevation, climatic conditions but potentially also landscape structure at a broader spatial scale than measured in our study, were more important than fine-scale landscape heterogeneity in explaining the composition of rice arthropod communities. Indeed, when we used elevation as a proxy for all regional-scale effects in the study regions, it explained the majority of variance (> 60%) in the assemblage structure based on the dissimilarity matrices (Fig. 2b, Appendix C.2 Supplementary material). The differences in the variability of arthropod composition among study regions can be further illustrated by the differences in variability of elevation and climate conditions in those regions (Appendix A Supplementary material).

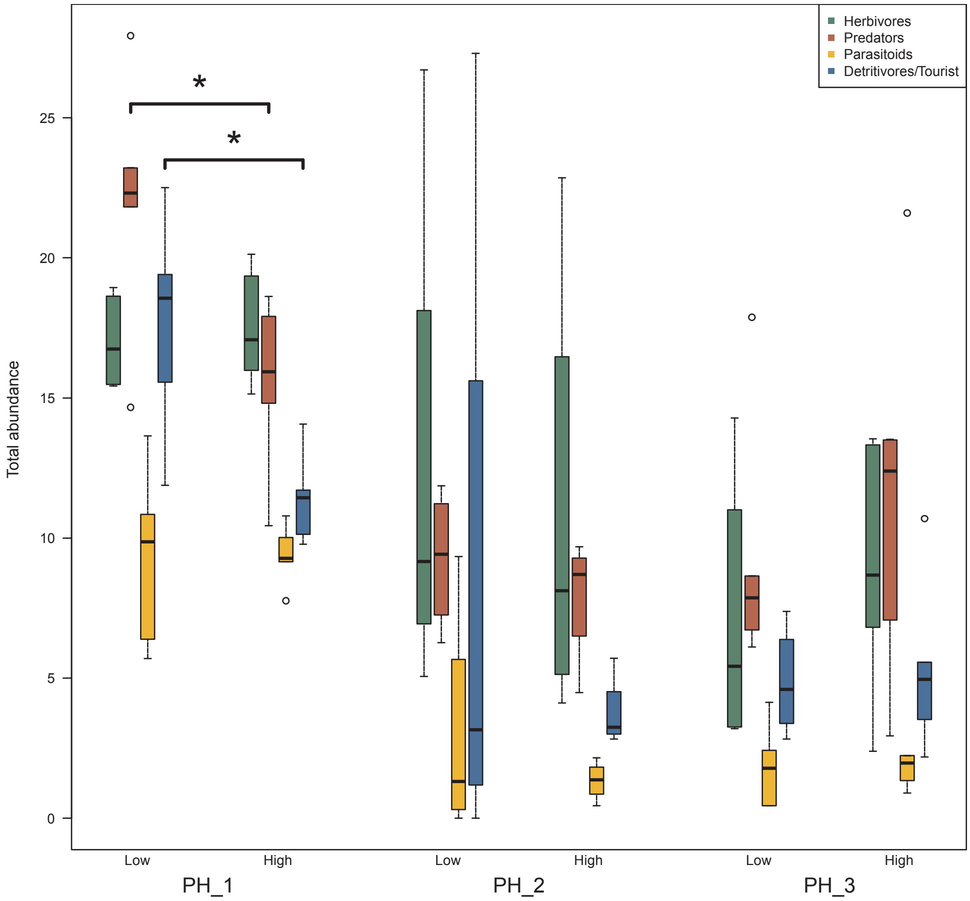

Fig. 6. Box-plots of the total mean abundance of functional groups for low heterogeneity sites ("Low") and high heterogeneity sites ("High") across the three regions (data derived from the blow-vac). Boxes show the median, 25th and 75th percentiles, maximum and minimum observations. Significant differences ($P < 0.05$) between low and high heterogeneity habitats are indicated by asterisks above and between boxes.

Moreover, not only did we find that total arthropod abundances decreased with increasing elevation, similarly as in Schoenly et al. (1996), but we also found that the total rarefied species richness decreased with increasing elevation. In addition, our results are in agreements with the conclusions of Hodkinson (2005); who showed that responses of species abundance to elevation are known to vary with taxa and location. While the abundance of most of the morphospecies such as *N. lugens*, *Nephotettix* spp., lycosids, linyphiids and chironomids decreased with elevation, two species, *S. furcifera* and *C. lividipennis,* found in high numbers in PH_3 were positively affected by elevation. These findings are also supported by a previous study showing that elevation is a limiting factor for the fitness of *N. lugens* (Settele, 1992).

Second, the investigated arthropod communities were potentially co-affected by other factors that are unique to each study region but were not accounted for in the design of our analysis. Our study was conducted in a real agricultural setting in which land-use intensity, cropping synchrony, pesticide inputs or other land management factors were not controlled. Although we assume that these factors did not vary systematically across the sites with high and low levels of fine-scale landscape heterogeneity, their specific character in each study region may have contributed to the high variability in our dataset and to the clear differences in the assemblage structure among study regions. In addition, the variability of elevation and climate was high among regions but low within regions. This further suggests that the effects of other factors specific to the regions, such as broad-scale landscape structure or the intensity of land use, cannot be fully disentangled from the overall regional effects without specifically controlling for them in the analysis.

Third, the scale and the binary distinction between sites with high and low heterogeneity may be insufficient to detect landscape effect on the rice arthropod fauna. While the differentiation of the two landscape heterogeneity levels around sampled fields was consistent for all regions, the broad-scale landscape structure among the three regions varies considerably (Burkhard et al., 2015). For example, the overall region PH_1 in Laguna is characterized by rice production landscapes with close proximity to numerous agricultural fields, gardens, ponds and semi-natural habitats. In contrast, rice fields in the region PH_2 of Nueva Ecija occupy over 95% of the land area, with each field being separated only by a network of terrestrial bunds combined with a low diversity of other habitats. Although the scale of a few hundred meters was previously found sufficient to show landscape effects in rice agroecosystems (Wilby et al., 2006), many rice invertebrates are known to migrate over considerably larger distances (e.g. Reynolds et al., 1999). In addition, the potential effects of a broad-scale landscape structure were likely confounded with the influence of environmental conditions that we accounted for in the analysis at the regional scale. Therefore, we suggest that future research should focus on a more detailed quantification of landscape heterogeneity (e.g. using metrics of landscape composition, configuration and intensity of use (Seppelt et al., 2016)) and examine its effect at multiple spatial scales that match the migratory abilities of the investigated rice arthropods.

We used two different sampling methods to assess the arthropod communities in the rice fields. The sweep net method was more efficient to sample leaf canopy arthropods such as chironomids, other dipterans, parasitoids and long-jawed orb weavers (Tetragnathidae). Samples taken with the sweep net were collected typically at the top of the rice canopy, since the lower surface of the plant was unreachable without damaging the plant. Arthropods that dwell low on the plant or on the water surface, i.e. *N. lugens*, dwarf spiders or lycosids, were caught in significantly greater numbers by the blow-vac. The combination of multiple sampling methods in rice fields is thus generally advised to properly assess arthropod biodiversity (Doxon et al., 2011). However, in our study, while differences in abundance of specific taxa were observed between sampling methods, both methods provided samples with similar species composition. This suggests that, in cases of limited time or resources, the use of only one method may be acceptable when the focus is on community composition rather than on species abundance.

5. Conclusion

We characterized and compared rice arthropod communities from three important rice production regions in the Philippines that differed in environmental conditions as well as in their level of landscape heterogeneity. Two principal insights are provided by our analyses. First, the rice agroecosystems in each study region had relatively distinct arthropod assemblages, likely reflecting specific environmental conditions or land management factors in the regions. Second, the effect of fine-scale landscape heterogeneity was identified only in one region and only for two functional groups and two morphospecies, suggesting that regional-scale effects rather than fine-scale landscape heterogeneity explain the composition of rice arthropod communities in the study area. To further disentangle the complex effects of broad-scale environmental drivers versus fine-scale landscape context on arthropod communities and the biocontrol services, future studies of rice agroecosystems should apply more complex procedures of quantifying the spatial structures of rice fields and the surrounding habitats and examine their effect at multiple spatial scales.

Acknowledgements

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Appendix A. Supplementary data

Supplementary data associated with this article can be found, in the online version, at http://dx.doi.org/10.1016/j.agee.2017.06.011.

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Appendix 6

Letter

Transparency and Control of Autonomous Wildness: A Reply to Galaz and Mouazen

Erle C. Ellis,[1,*]
Bradley Cantrell,[2] and
Laura J. Martin[3]

Galaz and Mouazen [1] argue that autonomous curation of wild places requires ‘algorithmic transparency, accountability, and public deliberation’. We completely agree. These are requirements for any fair and sustainable social endeavor, with or without algorithms. All conservation and design projects should meet these standards for open operation and stakeholder participation [2].

Nevertheless, we are unconvinced by their claim of a ‘new wilderness paradox’ in which increasingly automated curation of wild places produces a ‘stronger need for human supervision’. It is true that deep reinforcement learning systems can learn to do surprising things – many of them with undesirable outcomes. Yet the same is true of many well-intentioned human efforts to manage environments, like the once-common strategy of suppressing fires and other disturbances [3]. It is hard to see why the issues of bias and discrimination highlighted by Galaz and Mouazen are any different in automated systems than in those of any other human enterprise.

Autonomous curation of wild places is a risky social–ecological experiment with the potential for unexpected outcomes, both positive and negative. As with any experiment with potential for negative societal consequences, from self-driving cars to the reintroduction of wolves to the automated curation of wild places, it is essential to engage stakeholders, including the public, in transparent processes of governance in every phase of operation, from initial design to implementation, monitoring, and adaptive management [2]. But there is no reason why designed autonomy cannot incorporate such governance, and every reason why it should.

There are good reasons to be concerned by the loss of wildness and wilderness in the Anthropocene [4]. Yet demands for and on wild nature are increasing at the same time that cultural conceptions of these are expanding [5]. Through experiments in designed autonomy, much might be learned about the limits to human control of wild places and about the potential of wildness and wilderness to evolve far beyond these, even within the increasingly human biosphere of the Anthropocene.

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Letter

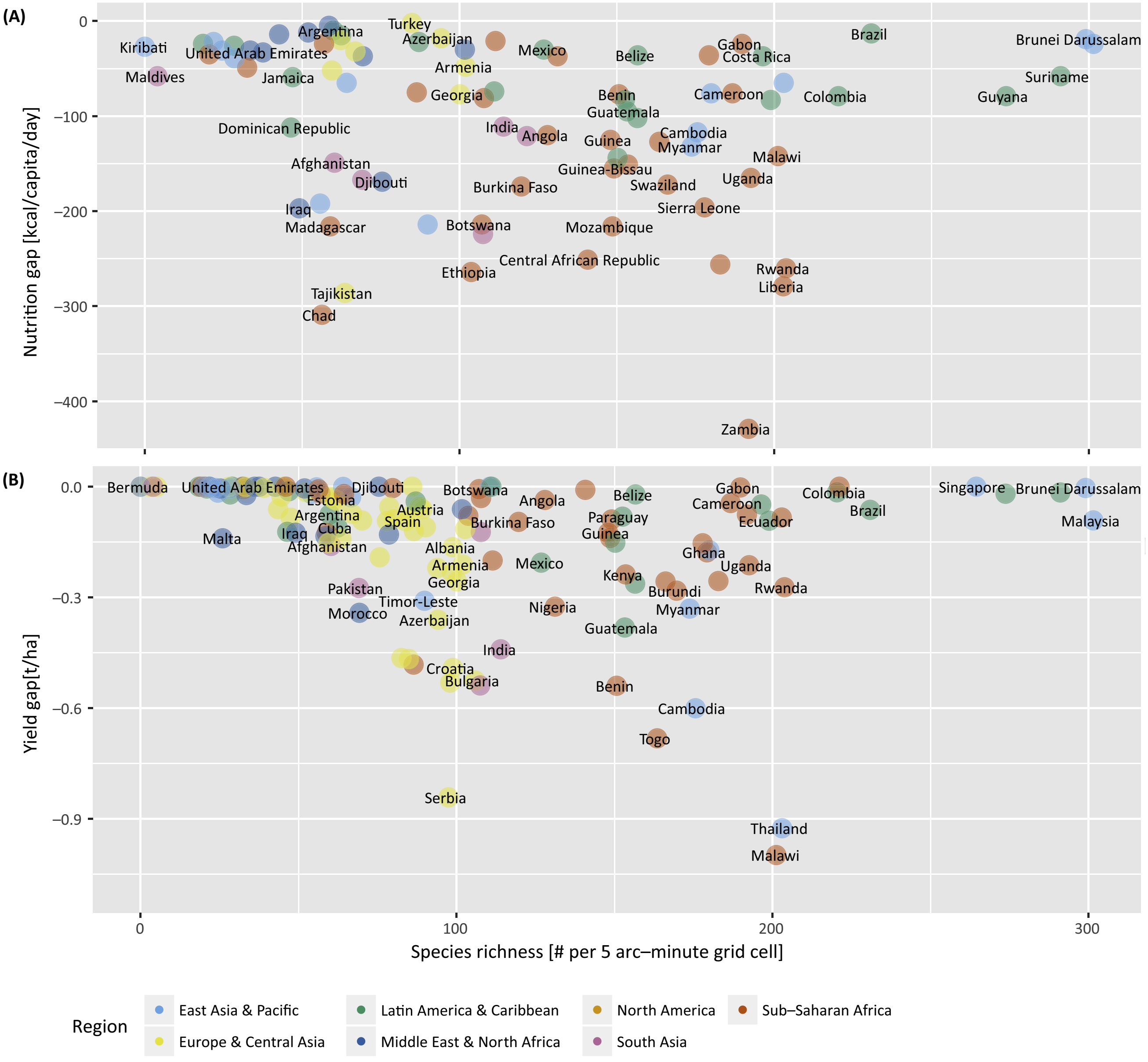
Searching for Win–Win Archetypes in the Food–Biodiversity Challenge: A Response to Fischer *et al.*

Ralf Seppelt,[1,2,3,*]
Michael Beckmann,[1] and
Tomáš Václavík[1,4]

There is no doubt about the urgent need to revise the current framing of the food–biodiversity challenge. Fischer *et al.* [1] make the laudable effort to conceptualize four archetypes of the biodiversity conservation and food security relation with examples from the global south. We applaud the authors for refraining from the frequently applied logic that a substantial increase in food production is needed to achieve food security and for suggesting a more nuanced conceptual narrative.

However, we would like to point out some concerns related to the ambiguity of the terms used, the realism of the proposed archetypes and the potential of the framework to identify how systems can be triggered to transition from one archetype to another.

First, rethinking the biodiversity–food security narrative requires a precise use of terms. The term ‘food security’ is multifaceted and encompasses, for example, food production, food sovereignty and nutrition. However, the framework the authors propose in their Figure 1 implies that food security is measurable as a one-



Trends in Ecology & Evolution

Figure 1. Ambiguity in the Application of the Framework Proposed by [1]. Illustration using national statistics on (A) nutrition gap versus species richness, and (B) yield gap versus species richness. Nutrition gap represents a 3-yrs average depth of nutrition deficit (2010-2012 in kcal/capita/day, based on national food balance sheets, prevalence of undernourishment, and household consumption and expenditure surveys, FAO[i]). Yield gap represents the difference between actual yield and the potential agroecological productivity, IIASA[ii]. Biodiversity is shown as the number of species in a 5-arc minute grid cells from IUCN range polygons averaged per country[iii].

dimensional variable. We see a risk that this simplification opens the door to misconceptions and misinterpretations when applying the framework. To illustrate these potential problems, we relate country-scale data for biodiversity (species richness) and two variables that have been used to represent food security (nutrition gap [2,3], yield gap [4]) in Figure 1. When comparing both plots it is clear that nutrition gap and yield gap lead to an entirely different interpretation about which countries have or have not achieved food security. Similarly, the term 'biodiversity' is multifaceted and summarizes various ecological patterns measured by different indicators (e.g., species richness, abundance-based measures, endemism, extinction risk, trait or functional diversity [5]).

Second, we are skeptical about the realism of the archetypes laid out, specifically of the proposed 'win–win' situation. It describes an agroecological system with outcomes benefitting both food security and biodiversity conservation goals. Again, the term 'win' for biodiversity remains undefined. While there is limited local evidence that increases in yields can come with an increase in or 'no harm' to biodiversity (e.g. [6]), recent global-scale syntheses find no evidence for 'win–win' patterns being ubiquitous (e.g., M. Beckmann et al., unpublished). However, selecting smallholder farms for the 'win–win' archetype might be a rather romanticized viewpoint. If they have the means and capacity, smallholder farmers will also likely turn towards conventional technologies to boost yields and thereby improve their livelihoods. The Philippine and Vietnam rice case is an excellent example, where pesticide applications in smallholder cropping systems increased considerably, due to the advertising of western agrochemical companies [7]. Thus, it is highly questionable that the 'win–win' case exists beyond highly localized examples, has the potential for a wider applicability and is stable on the longer run.

Third, we argue that the framework is lacking the dynamic perspective that would indicate how systems could be triggered to move between archetypes. The framework as it is described by Fischer *et al*. allows static labeling of production systems into one of four archetypes. The authors also provide examples of systems that have shifted between archetypes. However, the elaboration of the drivers and feedbacks that keep a system in its current state is lacking. For example, land-use intensification can have anything between severely negative or neutral [8,9] effects on biodiversity while the simultaneous positive effects on yield may scale very differently. We agree with the authors that especially the 'lose–lose' archetype is in need of transformation. While the anecdotal evidence provided is a decent starting point, a clear conceptualization of the drivers and feedbacks that generate alternative system outcomes is needed to help achieving such transformations.

In conclusion, Fischer *et al*. offer a substantial improvement over previously oversimplified approaches to the food–biodiversity challenge. Nevertheless, the proposed framework falls short in its applicability and would at least need to clearly define all used terms and consider the dynamic processes of change to effectively address problems of food security. Once more, this paper highlights the urgent need for a clear definition of the term 'food security' and its essential indicators, possibly following efforts to define essential biodiversity variables [10].

Resources

[i] http://faostat.fao.org/

[ii] http://www.gaez.iiasa.ac.at

[iii] http://www.iucnredlist.org/technical-documents/spatial-data

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Letter

We Need Qualitative Progress to Address the Food–Biodiversity Nexus: A Reply to Seppelt *et al.*

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We thank Seppelt *et al.* [1] for their thoughts on our paper, and welcome debate regarding how to best move forward in harmonizing food security and biodiversity conservation. We consider it useful to exchange ideas, including in areas where there may be disagreement, recognizing that reflection will help the

Appendix 7

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LETTER • **OPEN ACCESS**

Combined effects of climate and land-use change on the provision of ecosystem services in rice agro-ecosystems

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LETTER

Combined effects of climate and land-use change on the provision of ecosystem services in rice agro-ecosystems

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Keywords: vegetation modelling, ecosystem services, rice, Southeast Asia, land-use change, climate change

Supplementary material for this article is available online

Abstract

Irrigated rice croplands are among the world's most important agro-ecosystems. They provide food for more than 3.5 billion people and a range of other ecosystem services (ESS). 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 ESS, we applied the vegetation and hydrology model LPJmL to seven study areas in the Philippines and Vietnam. We quantified future changes in the provision of four essential ESS (carbon storage, carbon sequestration, provision of irrigation water and rice production) under two climate scenarios (until 2100) and three site-specific land-use scenarios (until 2030), and examined the synergies and trade-offs in ESS responses to these drivers. Our results show that not all services can be provided in the same amounts in the future. In the Philippines and Vietnam the projections estimated a decrease in rice yields (by approximately 30%) and in carbon storage (by 15%) and sequestration (by 12%) towards the end of the century under the current land-use pattern. In contrast, the amount of available irrigation water was projected to increase in all scenarios by 10%–20%. However, the results also indicate that land-use change may partially offset the negative climate impacts in regions where cropland expansion is possible, although only at the expense of natural vegetation. When analysing the interactions between ESS, we found consistent synergies between rice production and carbon storage and trade-offs between carbon storage and provision of irrigation water under most scenarios. Our results show that not only the effects of climate and land-use change alone but also the interaction between ESS have to be considered to allow sustainable management of rice agro-ecosystems under global change.

1. Introduction

Rice is the most consumed staple food for more than 3.5 billion people, with annual per capita consumption exceeding 100 kg in many Asian countries (Seck *et al* 2012). With a world population that is expected to increase from current 7.4 to 9.7 billion by 2050 (United Nations 2015) rice demand will continue to grow in the next decades. Even under ambitious scenarios of reducing food waste and distribution inequality (Ericksen *et al* 2009, Foley *et al* 2011), considerable increases in rice production will be necessary. These conditions place irrigated rice croplands among the world's most important agro-ecosystems (FAOSTAT 2014).

In addition to food production, rice agro-ecosystems simultaneously provide a number of other ecosystem services (ESS) that contribute to human well-being in rice producing regions as well as globally. These services include provision of fuel and fibre, 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, Spangenberg *et al* 2014). Maintaining essential ESS, while meeting the increasing rice demand at the same time, represents a major challenge for rice producing countries, especially in Southeast Asia (Greenland 2006, Laborte *et al* 2012).

Rice agro-ecosystems, however, are affected by a range of natural and anthropogenic drivers, such as land use and climate change. In these irrigated cropping systems (Václavík *et al* 2013), rice terraces and other crop fields are often expanded, typically at the expense of natural forests, leading to substantial forest loss and degradation (Castella and Verburg 2007, Fox *et al* 2012, Settele 1998). Although much of the original landscapes in Southeast Asia had already been transformed centuries ago (Pongratz *et al* 2008), when native vegetation was turned into agricultural land, large environmental impacts from land use expansion and intensification still prevail (Field *et al* 2014, Houghton and Hackler 1999, Torres *et al* 2014).

In the future, ESS in rice agro-ecosystems will be affected by further increasing atmospheric CO_2 and associated climate change, which includes increasing temperature and shifts in rainfall regimes (Howden *et al* 2007). In Southeast Asia, temperatures are projected to rise regionally between 1.5 and 4 K depending on the scenario (Nakićenović *et al* 2000), but even moderate warming will likely reduce rice yields in the next coming decades (Peng *et al* 2004, Welch *et al* 2010). Additionally, projections of future precipitation show changes in the amount of rainfall, regionally varying between -20% to $+20\%$ (Meehl *et al* 2007) and a gradual increment in winter monsoon rainfall in Southeast Asia under most climate change scenarios (Siew *et al* 2013). Despite the complex interplay of factors, the question how the multiple interactions of drivers and their expected changes affect future provision of important ESS in rice agro-ecosystems has not been consistently investigated.

Considering the need to maintain various ESS in rice agro-ecosystems under changing climate and land use, integrative approaches are required to assess environmental as well as social-ecological impacts. While previous studies examined the potential effect of climate change on rice production (Welch *et al* 2010, Peng *et al* 2004, Naylor *et al* 2007), it has not yet been systematically examined how the combination of both climate and land-use change simultaneously impacts multiple ESS in rice agro-ecosystems. Such integrative approach is crucial to better understand whether the interaction of both drivers amplifies their impact on ESS (both leading to decrease or both leading to increase, i.e. amplification effect) or whether the projected change in one driver can balance out the effect of the other driver (i.e. offset effect). In addition, understanding the relationships among multiple ESS is increasingly recognized as essential to ensure multi-functionality of landscapes (Bennett *et al* 2009, Rodríguez *et al* 2006, Bennett *et al* 2015). Therefore, we need to examine whether ESS are bundled in either positive ways (synergies) or negative ways (trade-offs) in a response to common drivers that affect the changes in multiple services at the same time (Bennett *et al* 2009).

In this study, we use an integrative simulation approach to assess the combined effect of projected climate and land-use change on a bundle of ESS in rice agro-ecosystems in seven study areas in the Philippines and Vietnam. These areas represent suitable investigation systems, as both countries doubled their rice yield in only 20 years, reaching 44 and 18 million t yr^{-1} in 2012, respectively (FAOSTAT 2014). At the same time, climate and land-use changes in these regions affect ESS that are crucial for local communities and the sustainable cultivation of rice (Settele *et al* 2015). We specifically focus on four ESS: (a) carbon storage, (b) carbon sequestration by the vegetation, (c) provision of irrigation water and (d) rice production, because these services are provided by the natural vegetation (a–c) or the cropland (d). Therefore, the ESS strongly depend on land-use change (d); they are connected to the carbon cycle/balance (a–b), thus closely related to climate change; and they are expected to show either synergistic effects (e.g. forest expansion increases carbon storage and provision of irrigation water) or trade-off effects (e.g. loss of forest due to rice field expansion reduces carbon storage).

Here, we address the following research questions: (1) What are the combined effects of projected climate and land-use changes on the provision of selected ESS in rice agro-ecosystems (amplification vs. offset effect)? (2) How do the relationships among multiple ESS change under scenarios of climate and land-use change (synergies vs. trade-offs)? To answer these questions we make use of LPJmL (Sitch *et al* 2003, Gerten *et al* 2004, Bondeau *et al* 2007, Rost *et al* 2008), a dynamic global vegetation and hydrology model (DGVM), and apply it at fine spatial resolution of 30 m to capture local heterogeneities in the seven study areas representative for rice production systems in Southeast Asia.

The novelty of our study lies first in quantifying the combined effects of climate and land-use change on multiple ESS and examining the ESS interactions in response to these two drivers. Second, for the first time, we apply a DGVM at the landscape scale, which enables us to provide more nuanced information for stakeholders and decision-makers in each study area. We briefly discuss the potential consequences of estimated changes for future socioeconomic development of the regions and the implications of our results as a first step to examine possible local adaptations to climate change.

2. Methods and data

2.1. Study areas

The study was conducted in seven study areas in the Philippines ($n = 3$) and Vietnam ($n = 4$, figure 1) as part of a larger research project on sustainable rice production (LEGATO; Settele *et al* 2015). All areas were

Figure 1. Overview of the seven study areas in the Philippines and Vietnam. Highland sites are Lao Cai (VN_3) and Ifugao (PH_3). Lowland sites are Laguna (PH_1), Nueva Ecija (PH_2), Hai Duong (VN_1), Vinh Phuc (VN_2) and Tien Giang (VN_4).

approximately 15 × 15 km in size, located along a gradient of elevation and land use (figure 2(*a*)). The proportion of agricultural land ranged from 19%–96% and the forest coverage ranged from 76% to 0% (table S1, available at stacks.iop.org/ERL/12/015003/mmedia). Because the climatic conditions and the coverage of agricultural land differ substantially in regions with different elevation, we grouped the study areas for the analyses into lowland sites and highland sites. The five lowland sites, Laguna (PH_1), Nueva Ecija (PH_2), Hai Duong (VN_1), Vinh Phuc (VN_2) and Tien Giang (VN_4), are situated below 500 m a.s.l. and show less than 35% of natural vegetation. The two highland sites, Ifugao (PH_3) and Lao Cai (VN_3), are situated above 500 m a.s.l. and have more than 60% of natural vegetation left. The two highland sites in particular have a long history of sustainable rice production with traditional cultivation methods, such as building of rice terraces and manual planting and maintaining of the rice crop (Settele 1998). For detailed descriptions of the study areas see table S1 as well as Klotzbücher *et al* (2015) and Burkhard *et al* (2015).

2.2. Simulating ecosystem services

We used the vegetation and hydrology model LPJmL to simulate future changes in carbon storage, carbon sequestration, provision of irrigation water and rice production (table 1) until the end of the 21st century. LPJmL is a process-based dynamic global vegetation model that explicitly simulates ecosystem processes with fully coupled water and carbon cycles. Natural vegetation is represented with nine generic plant functional types, while agricultural land is represented with 16 user-defined crops and pasture (Bondeau *et al* 2007). The model simulates plant growth, production and phenology of the natural and agricultural vegetation (see also SI section 1.2). LPJmL has been proved to reproduce current patterns of biomass production (Cramer *et al* 2001, Sitch *et al* 2003), also including managed land and crops (Bondeau *et al* 2007, Fader *et al* 2010, Rost *et al* 2008, Müller *et al* 2016), as well as water dynamics (Biemans *et al* 2009, Gerten *et al* 2004, 2008, Gordon *et al* 2004, Wagner *et al* 2003). Additionally, LPJmL has already been shown to provide quantitative assessments of valuable ESS (Metzger *et al* 2008, Karp *et al* 2015).

For calculating the main processes, controlling the dynamics of vegetation, LPJmL uses climate data (temperature, precipitation and cloud cover), atmospheric CO_2 concentration (prescribed by the SRES scenario, Nakićenović *et al* 2000) and soil type (FAO/IIASA/ISRIC/ISSCAS/JRC 2012) as input. To simulate crop production, LPJmL uses prescribed annual fractional coverage of several crop types, thus accounting for land-use change. We developed region-specific land-use scenarios covering the years until 2030 which integrated narratives of possible futures obtained from experts' interviews and a global trade model (see section 2.4). By applying climate and land-use change scenarios for the 21st century, we were able to assess changes in the provision of four ESS described in the following paragraph. Details on the use of model results in the ESS assessment can be found in table 1 and the SI section 1.2.

Carbon storage quantifies the capacity of the vegetation to store assimilated carbon (for up to several decades) above and below ground. It is significantly larger in forests compared to grasslands and can therefore also be used as an indicator for forest habitats, which provide additional ESS such as timber wood and fire wood extraction as well as habitat for plant and animal species. *Carbon sequestration* is the balance between the capacity of the vegetation to absorb

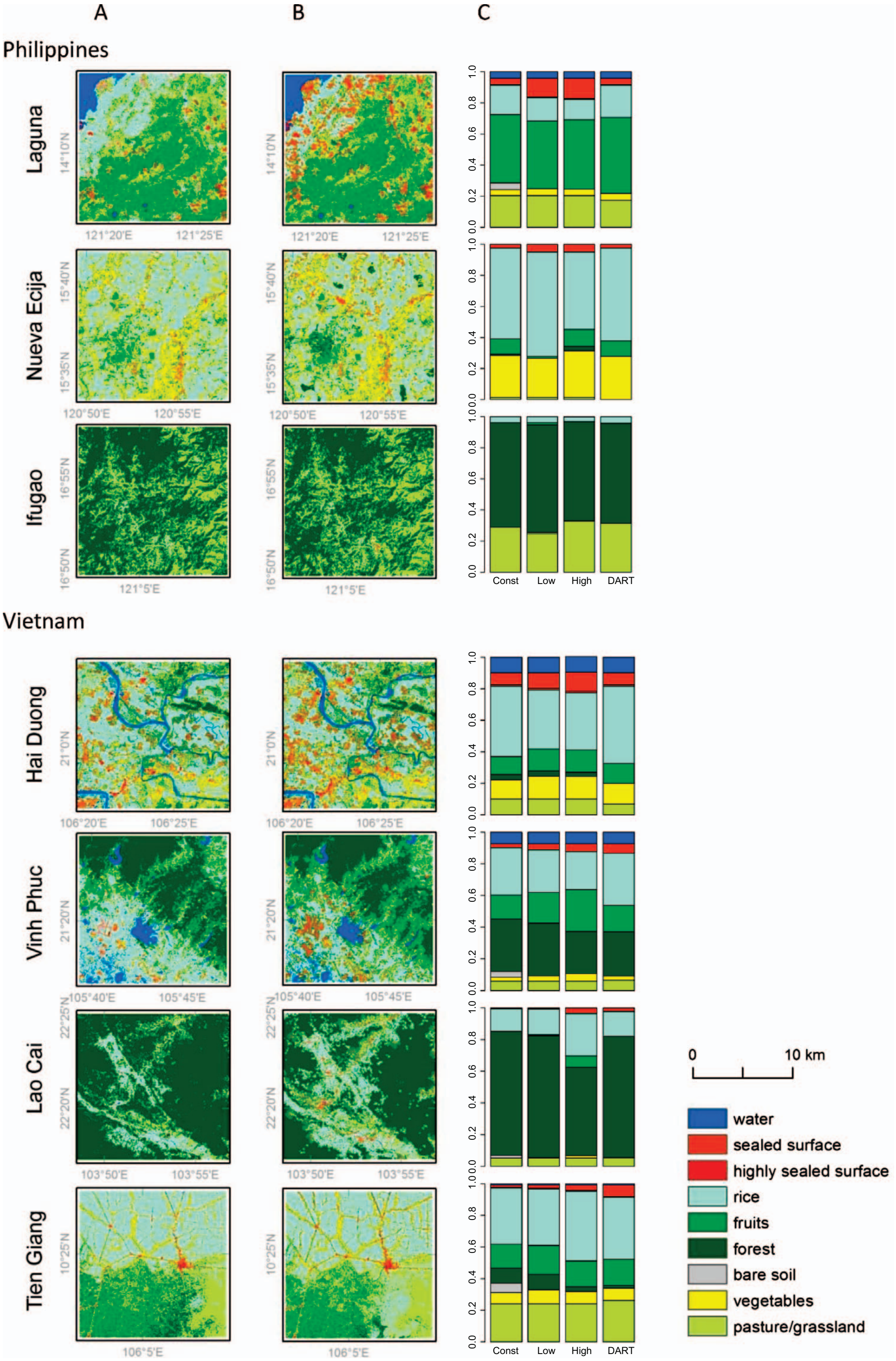

Figure 2. Land use classes in the seven study areas. (*a*) Observed land use class, (*b*) land use in 2030 in the expert scenario 'High-conversion' and (*c*) fraction of land use categories in 2030 in all land use change scenarios (Low-conversion, High-conversion and DART). The land use scenario 'Const' refers to the observed land use. Highland sites are Lao Cai (VN_3) and Ifugao (PH_3). Lowland sites are Laguna (PH_1), Nueva Ecija (PH_2), Hai Duong (VN_1), Vinh Phuc (VN_2) and Tien Giang (VN_4).

carbon from the atmosphere (via photosynthesis) and to respire carbon from living tissue (via autotrophic respiration) and dead organic material (via heterotrophic respiration); in LPJmL both are calculated on a daily basis. Changes in temperature and precipitation affect both processes—photosynthesis and respiration, thus controlling this ecosystem service and making it sensitive to climate change. The amount of *irrigation water* is an indicator for potential rice production, fish production and river (flow) maintenance (Steffen *et al* 2015). For our estimation we use the amount of water before LPJmL reduces it by irrigating crops. It therefore represents the potential irrigation that is restricting crop growth. *Rice production* itself describes its provisioning potential under future climate and land use change.

Table 1. Overview of the selected ecosystem services.

Ecosystem service (ESS)	Short definition	Indicator (model output)	Unit	Reaction to climate change	Reaction to land use change (deforestation)
Carbon storage	Amount of carbon that is stored in above and below ground living and dead biomass.	Sum of carbon stored in vegetation, litter and soil.	[kg C m^{-2}]	+ΔT causes higher heterotrophic respiration and lower photosynthesis causes lower carbon storage; +ΔT on high altitudes causes sparse vegetation gets more dense.	fewer forests cause less carbon storage
Carbon sequestration	Amount of carbon that is sequestered by natural vegetation and crops.	Annual sum of net primary production and carbon allocated in seeds, reduced by the annually respired carbon (heterotrophic respiration).	[g C m^{-2} yr^{-1}]	+ΔT causes higher respiration causes lower carbon sequestration.	more crops cause higher carbon sequestration
Irrigation water	Amount of water that is available for irrigation (while maintaining the environmental flow requirements of rivers, which is 45%–75% of the available water (Steffen *et al* 2015); amount before crop irrigation is calculated in the model.	25% of the annual sum of run-off water	[mm yr^{-1}]	+ΔT causes higher evaporation causes less irrigation water; +ΔP causes more irrigation water.	negligible
Rice production	Amount of rice harvested in the study area.	Carbon harvested from rice plants multiplied by the factor 1/0.45 to convert from carbon to biomass.	[t yr^{-1}]	+ΔT causes lower yield.	more rice area causes more rice production

2.3. Climate data and scenarios

To estimate future changes in the provision of examined ESS, we applied climate scenarios from the general circulation model MPI-ECHAM5, under the two SRES emission scenarios A2 and B1 (Nakićenović *et al* 2000), which were bias-corrected with CRU TS 3.0 (Harris *et al* 2014). We chose these two SRES scenarios because they cover two extreme emission trajectories (Meehl *et al* 2007). In the SRES B1 scenario an increase in temperature of about 1.5K–2K and a change in precipitation of ±10% are projected for our study areas. In the more severe A2 scenario the temperature is projected to increase by 3K–4K, while the precipitation will increase by about 10% (Christensen *et al* 2007).

To capture local climate heterogeneity in our study areas, we first scaled down the original 0.5 arc-degree global (observed and projected) climate data (see following paragraph) to a 30 m resolution using inverse distance interpolation (Shepard 1968). Second, we corrected the temperature and precipitation data according to the elevation in the study area with a temperature lapse rate of −5/1000 (5 K reduction per 1000 m elevation increase) and a precipitation lapse rate of 0.05/100 (5% increase per 100 m elevation increase) (Olea 1999). We validated our method against observed data from 25 meteorological stations close to our study areas. Details on the datasets for downscaling and validation and the validation results can be found in the SI section 1.3.

Finally, we applied our downscaling method to the climate projections. All climate scenarios are provided as monthly data which are then linearly interpolated to quasi-daily values in the LPJmL model. Atmospheric CO_2 concentration has been fixed to a level of 369.5 ppm to exclude the strong fertilization effect in LPJmL, which is caused by a lack of nutrient limitations in the model.

2.4. Land use data and scenarios

To describe the current land use conditions in each study area, we used previously developed land use classification, based on SPOT5 satellite images (www.astrium-geo.com/en/143-spot-satellite-imagery) obtained for the years 2009–2011 (Burkhard *et al* 2015). This remote sensing image interpretation distinguished nine land use categories: water, bare soil, sealed surface, highly sealed surface, rice, fruits plantations, vegetable fields, forest, and pastures/grassland (figure 2(*a*), table S1). We rescaled the land-use maps from the original 2.5 m resolution to a 30 m resolution.

Three potential land-use change (LUC) scenarios were developed, covering a wide range of possible developments until the year 2030. Two scenarios were developed in close cooperation with social scientists and local stakeholders (farmers, land owners, etc.) in the study area. These scenarios were specifically tailored for the study areas to provide insights into possible future developments for rice, pasture, settlements and natural forest, accounting for local/country-specific regulations and historical land-use legacies. We asked our local experts for one more conservative and one more extreme assessment to provide a range of potential future trajectories. From these expert opinions, narratives were developed that then built the basis of our spatially and temporally explicit land-use scenarios. The 'Low-conversion' scenario represents low rates of LUC, in contrast to the 'High-conversion' scenario presenting high rates of LUC (for scenario overview and corresponding trends see table S6). The third scenario, 'DART', examines how global land-use change patterns, based on the world economy DART-BIO model (Calzadilla *et al* 2014), might affect the small-scale study areas. The quantity and location of change provided by the LUC scenarios were calculated for each land-use category on a yearly basis based on a set of rules, using ArcGIS 10.3 (ESRI, Redlands, CA) and Python (Python Software Foundation, version 2.7, www.python.org). For details see supplementary section 1.5. Figure 2(*b*) shows an example of the High-conversion scenario for the projected situation in the year 2030. The scenario without changes in land use ('Const') represents the control situation.

2.5. Simulation experiments and analyses

We conducted simulations from 1901 until 2099, preceded by a 1000 year spin-up period in which climate data from 1901–1930 have been recycled, to initialize the vegetation from bare ground and to bring the carbon pools into equilibrium. The soil input was based on data from the Harmonized World Soil Database (FAO/IIASA/ISRIC/ISSCAS/JRC 2012). From 1901 until the year of the SPOT land use data, the land use forcing was kept constant, assuming only minor changes in the fraction of forest/cropland in the last century (Pongratz *et al* 2008). Although some changes in cropland until 1992 were identified by the large-scale estimates of Pongratz *et al* (2008), Settele *et al* (1998) suggest that in the Philippines and in Vietnam land-use changes occurred mostly at a local scale, including shifts in the distribution of rice fields and in abandonment or establishment of terraces. Therefore, keeping the land-use input constant for the 20th century is a reasonable assumption, and the uncertainties in the assumed past trends had only minimal effect on the projected changes of ESS. From the year of the SPOT data onwards the different trends from the LUC and the 'Const' scenarios were applied until 2030. Realistic scenarios of LUC for more than 20 years are difficult to develop. However, the time until 2030 is not long enough to see large climate change effects (Naylor *et al* 2007). Therefore, we continued our simulation until the end of the century to further assess the combined effects of climate and land-use change, while keeping the land use constant after 2030.

To analyse changes in the studied ESS (section 2.2), we calculated the annual average (2000–2099) smoothed as a 10 year running mean. The effect of climate change alone can be assessed by analysing the constant land-use change scenario (Const). To estimate the LUC effects alone we subtracted the Const-scenario results from the results of each LUC scenario simulation (Low-conversion, High-conversion, and DART).

To quantify synergies and trade-offs among projected ESS we calculated the Pearson correlation coefficient for each pair of services. This correlation provides information about the way (positive or negative) and the degree in which the services relate to each other. Therefore it helps identifying synergies (significant positive correlation) and trade-offs (significant negative correlation) between ESS in terms of their response to climate and land-use drivers. For correlations under combined scenarios of climate and land-use change we used the 10 year running mean of the period 2000–2099 and for correlations under LUC only we used the 10 year running mean of the period 2010–2030, because the land-use scenarios end in 2030.

3. Results

For most ESS and scenarios, combined climate and land-use change reduced the provision of ESS when compared to the baseline period 2001–2010 (figures 3 and 4 for SRES A2; figure S4 and figure S5 for SRES B1). With the exception of irrigation water, climate change alone caused a considerable decrease in ESS by the end of this century (figure 3 (black boxes, representing no land-use change) and figure 4(*a*)). In contrast, the response to LUC depended largely on the considered land-use scenario (see also figure S2 table S8 for absolute values).

Carbon storage declined by 5%–30% by the end of the century, with the highest decrease in the lowland sites under the DART scenario (figure 3(*b*), light-grey boxes). The overall negative effect of climate change was typically amplified by LUC, especially under the more drastic High-conversion scenario (figure 4(*c*)). However, in the case of highland sites under Low-conversion scenario (figure 3(*a*) and figure 4(*b*)), LUC did partially offset the negative effect of projected climate change on carbon storage.

Carbon sequestration showed a slight overall decrease by 2099 (figure 3), although it showed mid-century increases in the lowland sites and continued to increase until the end of the century in the highland sites under the High-conversion scenario (+25%). The periodicity in this ESS, as shown in figure 4, is caused by the climate input (e.g. El Niño events or repeating climate characteristics), which has direct effects on the temperature and therefore influences the carbon sequestration. Nevertheless, the overall trend is negative towards 2099. LUC was only able to temporarily offset the negative effects of climate change, especially

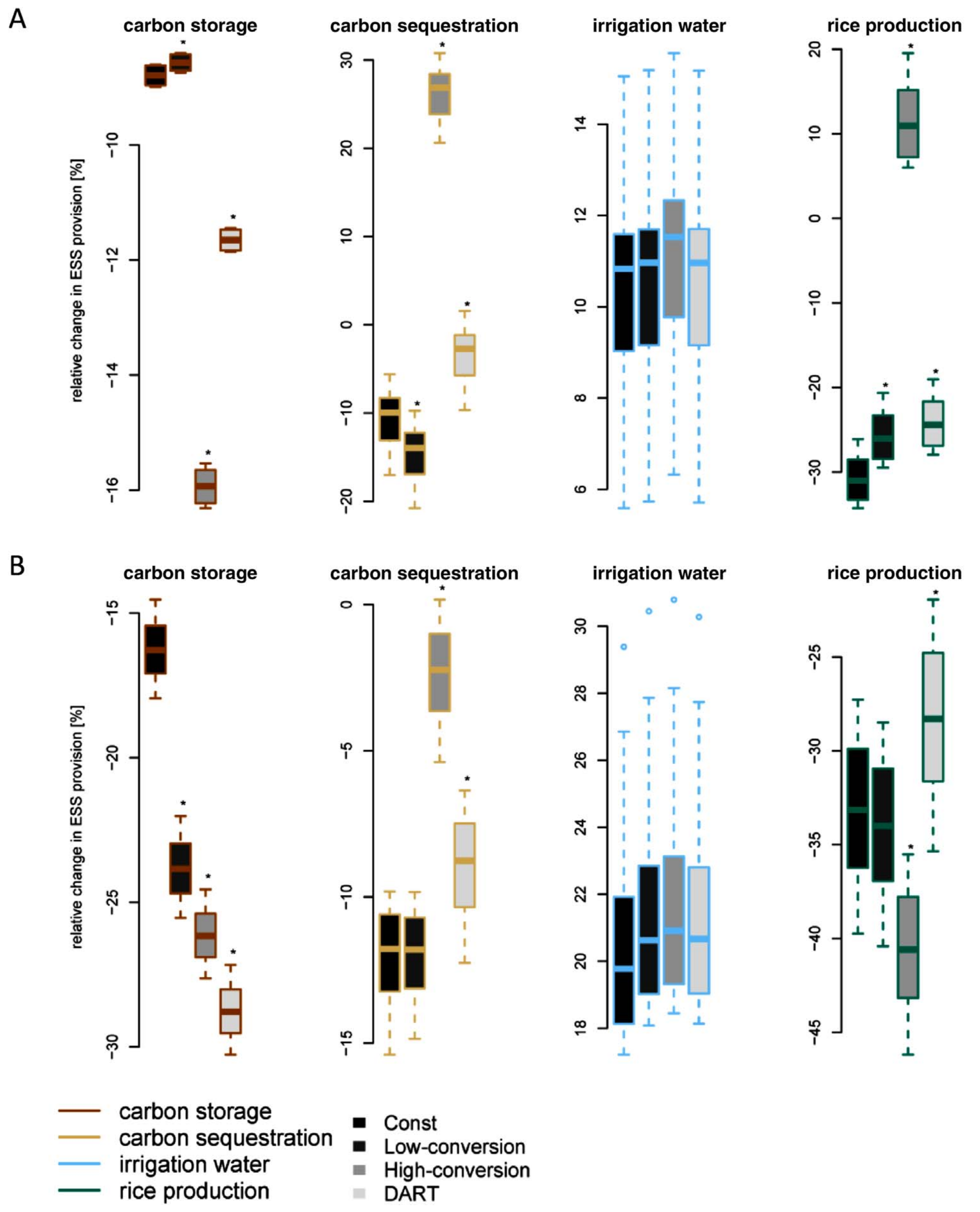

Figure 3. Combined effects of climate and land-use change shown as relative change in the provision of four ESS (compared to the baseline period 2001–2010, indicated by the colors) under the SRES scenario A2. Boxplots compiled for 2080–2099 in (*a*) highland sites and (*b*) lowland sites. Different land-use scenarios indicated by different gray filling of the boxes. Asterisks indicate a significant difference to the constant land use scenario (Const), $p < 0.05$.

when greater shifts in land use were assumed, as in the High-conversion scenario (figure 4(*c*)).

The provision of irrigation water showed an overall positive trend with mean increases of +11% in highland sites (figure 3(*a*)) and +21% in lowland sites (figure 3(*b*)). This trend was driven mainly by climate change with only marginal amplification by LUC, irrespective of the LUC scenario. Like the carbon sequestration, irrigation water shows periodically repeating patterns, which can also be explained by the climate input (primarily precipitation). These two services are estimated on a short term (few months) and are therefore more sensitive to short-term fluctuations than the carbon storage and the production of rice.

In contrast to irrigation water, rice production showed a clear response to LUC. While the combination of both drivers had mostly negative effects on rice production in the long term, leading to losses typically between 20% and 40% by 2099, changes in land use in the highlands were able to offset these effects in the first decades of the century. In the High-conversion scenario, the increase by 2030 was strong enough (50%) to override climate change effects even after the period of assumed land-use change, leading to overall 10% increase by 2099 (figure 3(*a*) and figure 4(*c*)). The strong decrease in rice production after 2030 is caused solely by the negative effects of climate change, with higher minimum temperatures reducing yields (Peng *et al* 2004, Welch *et al* 2010). In the lowland sites, where options for cropland expansions are limited, LUC amplified climate-change induced decline in rice production. All rice production estimates

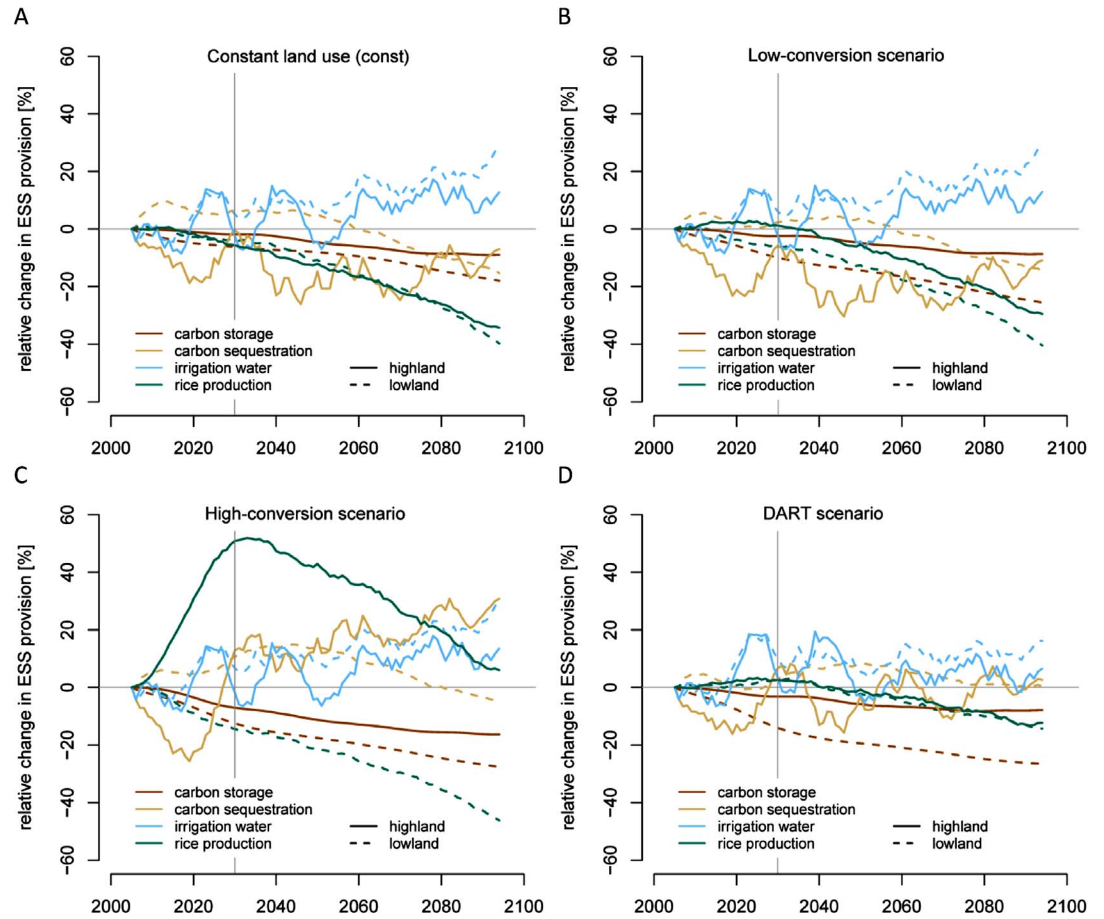

Figure 4. Time series of combined effects of climate and land use change shown as relative changes in the provision of four ecosystem services (compared to the baseline period 2001−2010) under the SRES scenario A2. The panel shows ESS dynamics for constant land use ((*a*), representing climate change alone) and the three different land use change scenarios ((*b*) low conversion, (*c*) high conversion, (*d*) conversion according to DART) (10 year running mean). The grey line indicates the last year of the land-use change scenarios.

were validated against on-site measurements. The results of this analysis showed that the simulated yields were comparable to measured yields as well to the yields reported by farmers (table S5).

The correlation analysis, using Pearson correlation coefficient *r*, identified whether the effects of climate and land-use change on provision of multiple ESS were in the same direction for two services (positive correlation indicates synergy, i.e. enhancing both ESS or diminishing both ESS) or in opposite directions (negative correlation indicates trade-off, i.e. diminishing one service while enhancing the other). The ‘LUC only’ columns in tables 2(*a*) and (*b*) show the effects of land-use change alone, while the other columns show the combined effects of climate and land-use change. Most pair-wise relationships were significant (table 2), especially for the lowland sites (table 2(*b*)), suggesting clear synergies and trade-offs among individual ESS. In lowlands, carbon storage and rice production, among others, were always positively correlated (synergy) with *r* ranging between 0.790 and 0.999, while carbon storage and irrigation water in lowlands were mostly negatively correlated (trade-off) with *r* ranging between −0.989 and 0.998 and nearly independent of the climate and the land-use change scenario. For some services the relationship changed slightly depending on (a) the climate scenario, showing large differences between the climate-change scenarios, e.g. irrigation water and rice production in highlands, or on (b) the LUC scenario, e.g. carbon sequestration and carbon storage in highland, or on (c) a combination of both drivers, e.g. carbon sequestration and irrigation water in lowlands.

4. Discussion

Our results show that future changes in climate and land use lead to significant declines in the provision of three out of four quantified ESS by the end of the century. With the exception of irrigation water, whose provision increases due to increased precipitation levels, climate change reduces the supply of the considered ESS. The additional effect of LUC is smaller (figure S3). Where unmanaged land is still available, new land conversion may allow partially offsetting negative climate change effects, but only at the expense of carbon storage in natural vegetation and therewith at the expense of natural habitat.

The future climate-induced reduction in carbon storage is mainly caused by lower photosynthesis rate

Table 2. Pearson correlation coefficient between the ecosystem services for highland sites (A) and lowland sites (B). Correlation under land use change and climate change (either under SRES A2—CC$_{A2}$, or SRES B1—CC$_{B1}$) together for 2000–2099, or land-use change only (LUC only) for 2000–2030 Order of land use scenarios within climate scenarios is Const, Low-conversion, High-conversion, DART. Red indicates a positive correlation (> +0.5), while blue indicates a negative correlation (< −0.5). Significance indicated by ∗ for $p < 0.05$ and ∗∗ for $p < 0.01$.

A

carbon storage	CC$_{A2}$ +LUC	CC$_{B1}$ +LUC	LUC only	carbon storage/ carbon sequestration: more sensitive to **LUC** than to **CC** scenario			carbon storage/ irrigation water: more sensitive to **CC** than to **LUC** scenario			carbon storage/ rice production: more sensitive to **LUC** than to **CC** scenario		
	1(Const)	1	NA									
	1(Low)	1	1									
	1(High)	1	1									
	1(DART)	1	1									
carbon sequestration	**CC$_{A2}$ +LUC**	**CC$_{B1}$ +LUC**	**LUC only**	CC$_{A2}$ +LUC	CC$_{B1}$ +LUC	LUC only	carbon sequestration/ irrigation water: more sensitive to **LUC** than to **CC** scenario			carbon sequestration/ rice production: sensitive to **LUC** scenario		
	+0.284**	+0.185	NA	1	1	NA						
	+0.315**	+0.247*	+0.617*	1	1	1						
	−0.890**	−0.889**	−0.984**	1	1	1						
	−0.266*	−0.395**	−0.960**	1	1	1						
irrigation water	**CC$_{A2}$ +LUC**	**CC$_{B1}$ +LUC**	**LUC only**	**CC$_{A2}$ +LUC**	**CC$_{B1}$ +LUC**	**LUC only**	CC$_{A2}$ +LUC	CC$_{B1}$ +LUC	LUC only	irrigation water/ rice production: more sensitive to **CC** than to **LUC** scenario		
	−0.551**	−0.001	NA	−0.256*	−0.169	NA	1	1	NA			
	−0.566**	−0.063	+0.741**	−0.266*	−0.234*	+0.562	1	1	1			
	−0.573**	−0.160	−0.961**	+0.442**	+0.095	+0.925**	1	1	1			
	−0.561**	−0.102	−0.829**	+0.033	−0.103	+0.938*	1	1	1			
rice production	**CC$_{A2}$ +LUC**	**CC$_{B1}$ +LUC**	**LUC only**	**CC$_{A2}$ +LUC**	**CC$_{B1}$ +LUC**	**LUC only**	**CC$_{A2}$ +LUC**	**CC$_{B1}$ +LUC**	**LUC only**	CC$_{A2}$ +LUC	CC$_{B1}$ +LUC	LUC only
	+0.980**	+0.944**	NA	+0.212*	+0.138	NA	−0.552**	−0.082	NA	1	1	NA
	+0.944**	+0.895**	−0.307	+0.144	+0.139	−0.814**	−0.525**	+0.040	−0.067	1	1	1
	+0.001	−0.518**	−0.996**	+0.037	+0.533**	+0.965**	−0.052	+0.424**	+0.967**	1	1	1
	+0.901**	+0.834**	−0.998**	−0.337**	−0.328**	+0.951**	−0.514**	+0.086	+0.804**	1	1	1
	carbon storage			**carbon sequestration**			**irrigation water**			**rice production**		

B

carbon storage	CC$_{A2}$ +LUC	CC$_{B1}$ +LUC	LUC only	carbon storage/ carbon sequestration: more sensitive to **LUC** than to **CC** scenario			carbon storage/ irrigation water: more sensitive to **CC** than to **LUC** scenario			carbon storage/ rice production: more sensitive to **LUC** than to **CC** scenario		
	1(Const)	1	NA									
	1(Low)	1	1									
	1(High)	1	1									
	1(DART)	1	1									
carbon sequestration	**CC$_{A2}$ +LUC**	**CC$_{B1}$ +LUC**	**LUC only**	CC$_{A2}$ +LUC	CC$_{B1}$ +LUC	LUC only	carbon sequestration/ irrigation water: sensitive to **CC** and **LUC** scenario			carbon sequestration/ rice production: sensitive to **CC** and **LUC** scenario		
	+0.918**	+0.782**	NA	1	1	NA						
	+0.831**	+0.652**	−0853**	1	1	1						
	+0.272**	−0.472**	−0.985**	1	1	1						
	+0.537**	−0.074	−0.947**	1	1	1						
irrigation water	**CC$_{A2}$ +LUC**	**CC$_{B1}$ +LUC**	**LUC only**	**CC$_{A2}$ +LUC**	**CC$_{B1}$ +LUC**	**LUC only**	CC$_{A2}$ +LUC	CC$_{B1}$ +LUC	LUC only	irrigation water/ rice production: sensitive to **CC** scenario		
	−0.901**	−0.628**	NA	−0.830**	−0.487**	NA	1	1	NA			
	−0.906**	−0.621**	−0.917**	−0.822**	−0.580**	+0.618*	1	1	1			
	−0.906**	−0.644**	−0.984**	−0.391**	+0.197	+0.957**	1	1	1			
	−0.899**	−0.637**	−0.999**	−0.662**	−0.274**	+0.939**	1	1	1			
rice production	**CC$_{A2}$ +LUC**	**CC$_{B1}$ +LUC**	**LUC only**	**CC$_{A2}$ +LUC**	**CC$_{B1}$ +LUC**	**LUC only**	**CC$_{A2}$ +LUC**	**CC$_{B1}$ +LUC**	**LUC only**	CC$_{A2}$ +LUC	CC$_{B1}$ +LUC	LUC only
	+0.981**	+0.963**	NA	+0.962**	+0.853**	NA	−0.877**	−0.549**	NA	1	1	NA
	+0.964**	+0.986**	+0.995**	+0.933**	+0.724**	−0.829**	−0.893**	−0.598**	−0.936**	1	1	1
	+0.980**	+0.996**	+0.999**	+0.443**	−0.431**	−0.976**	−0.920**	−0.675**	−0.989**	1	1	1
	+0.821**	+0.790**	−0.996**	+0.866**	+0.308**	+0.916**	−0.809**	−0.380**	+0.998**	1	1	1
	carbon storage			**carbon sequestration**			**irrigation water**			**rice production**		

and higher respiration under elevated temperatures (Ryan 1991). This trend is further amplified because under most LUC scenarios the extent of natural vegetation decreases, and therewith also carbon stored in forests. In contrast to carbon storage, the sequestration of carbon is likely to increase with projected LUC in all cases, except for the High-conversion scenario in highland sites. Carbon sequestration represents the ability of the vegetation to absorb carbon. In systems at equilibrium, such as old growth forest, the maintenance respiration is higher than in agricultural systems, which leads to a lower NPP. As a consequence, the carbon sequestration in crop systems is much higher, although trees have larger leaf area available for photosynthesis. Therefore, the expansion of agricultural areas with fast growing rice and vegetables, which exhibit low rates of maintenance respiration (Ryan 1991), will lead to an increase in carbon sequestration. This is especially evident in the highland sites under the High-conversion LUC scenario. In these cases, large forest-to-cropland conversions are expected. This changes the ratio of trees (less trees, with lower carbon sequestration) to crops (more crops, with higher carbon sequestration), causing a substantial offset of the negative climate change impact by the year 2100.

The availability of water for irrigation is a major prerequisite for rice production. Despite the projected increase in its provision under all considered scenarios, climate change leads to a decline in rice production which is in agreement with previous studies (Peng *et al* 2004, Welch *et al* 2010). Where rice production can only be increased through expansion of rice terraces as projected by our LUC scenarios in the highland sites, trade-offs to carbon storage emerge due to significant losses of natural forest vegetation, however this trade-off can only be assessed by considering land-use change only. In the lowland sites, where nearly no additional land is available for agricultural expansion and the extent of settlements is likely to grow, we project an additional decline in rice production compared to climate change only (figures 3 and 4).

In addition to the effects arising from land available for conversion, the observed differences that we found between highland and lowland sites for most projections of ESS can be mainly attributed to the lower cropland coverage and lower temperatures in the highland compared to the lowland sites. The negative effects of climate change are less pronounced in the highland sites, because the increase in carbon storage in the highest altitudes caused by a temperature increase can compensate for losses in lower lying areas. This positive effect, however, has its limitation due to the decreasing available area in higher altitudes. Among our study areas, Lao Cai (VN_3) is the highest in elevation and would benefit most from increasing temperatures, since the mountain tops are only sparsely covered with vegetation. The other highland site (Ifugao, PH_3) is at lower elevation and would benefit less because the mountain tops are already covered with vegetation.

Our findings narrow the scope of potential land-use options that can be adopted to reduce the threat posed by future climate change to ESS in rice agro-ecosystems. The three LUC scenarios developed for this study allowed us to assess a range of such options. However, in all cases the potential of land use for local adaptation to climate change is limited. In the case of rice production, for example, the expansion of rice terraces would have to be drastic (see also figure 2(*c*) Lao Cai) to even partially offset the impact of climate change. In addition, our results indicate that local policies promoting such type of LUC might work only in the horizon of a few decades, but alone would be insufficient to mitigate climate change in the long term. Therefore, local policies aiming at sustainable rice production and food security in the face of climate change should consider other adaptation strategies suitable for rice agro-ecosystems, including crop diversification and rotation, the use of stress-tolerant rice varieties, adjustments of sowing season, or methods of ecological engineering (Banerjee *et al* 2016, Kumar 2016, Li *et al* 2015).

Managing rice agro-ecosystems for multiple ESS is even more challenging because several ESS are often provided by the same land-use type but they do not always respond the same way to underlying drivers (Haase *et al* 2012). We identified such trade-offs, e.g. between irrigation water and all other ESS, as the provision of irrigation water shows consistently positive response to combined climate and land-use change effects while the provision of other ESS declines. Similarly, trade-offs between rice production and carbon storage were found as a response to LUC especially in highland regions of Lao Cai (VN_3) and Ifugao (PH_3) (table 2(*a*)). However, the trade-offs between ESS are often not obvious because both ESS considered are heavily influenced by climate change, which masks the effects of LUC (table 2(*a*)). The identified trade-off between rice production and carbon storage—under land-use change only—corroborates findings by Burkhard *et al* (2015) who documented trade-offs between crop production and a range of other ESS, including biodiversity, crop pollination and recreation. Especially when high rates of LUC are assumed, the encroachment of crop fields in natural forests not only leads to a reduction in carbon storage but also reduces potential timber and firewood extraction and affects habitat for plant and animal species. Therefore, we caution that, although we quantified the response of arguably the most important ESS in rice agro-ecosystems, more detailed and context-specific assessments are needed to understand the possible outcomes of climate change and land management strategies (Castonguay *et al* 2016). In addition to rice production, these assessments should consider other non-provisioning ecosystem services, impacts on biodiversity, resilience of rice agro-ecosystems, and cultural and societal implications (Förster *et al* 2015).

5. Conclusion

Understanding the effects of climate and land-use change on the provision of ESS and identifying synergies and trade-offs in their responses is crucial for maintaining multi-functional production systems. Our study of rice agro-ecosystems showed that the trend in the ESS provision is relatively clear if we consider climate change only, but it becomes more complex when LUC is included, leading to opposite trends depending on the severity of environmental change and the study area. In general, climate change and LUC reduced ESS provision in most of the considered scenarios, both in highland (10 out of 16) and lowland sites (12 out of 16). Only high land-conversion rates were able to partially offset negative climate change effects. With a projected temperature increase for the Philippines and Vietnam of up to 4 K by 2100, rice production can likely be maintained only at the expense of natural vegetation, whose reduction is typically accompanied by loss of native habitat and biodiversity with poorly understood cultural and societal implications. Therefore, locally specific land-use policies and development plans have to consider not only the provision of crops but also regulating and cultural services to maintain future human well-being and natural resources of rice agro-ecosystems in Southeast Asia. This study illustrates the importance of considering small scale land-use patterns and climate-change scenarios to assess the complex interactions of several ESS and to inform local decision makers and stakeholders.

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Appendix 8

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RESEARCH ARTICLE

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Landscape composition, configuration, and trophic interactions shape arthropod communities in rice agroecosystems

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Abstract

1. Increasing landscape heterogeneity of agroecosystems can enhance natural enemy populations and promote biological control. However, little is known about the multiscale effects of landscape heterogeneity on arthropod communities in rice agroecosystems, especially in combination with trophic interactions.
2. We examined for the first time how landscape heterogeneity, measured by four independent metrics of landscape composition and configuration at three spatial scales, affected species abundance and species richness of rice arthropods within four functional groups and the abundance of the most common species at 28 sites in the Philippines. We additionally examined the influence of trophic interactions among these functional groups.
3. We found that both the compositional and configurational landscape heterogeneity in combination with trophic interactions determined the structure of rice-arthropod communities. Herbivore abundance decreased with increasing landscape diversity. The abundance of parasitoids and species richness of both parasitoids and predators increased with the structural connectivity of rice bunds. Fragmentation of the rice landscape had a clear negative effect on most arthropod groups, except for highly mobile predatory arthropods. Abundance of common predators and detritivore species decreased with increasing complexity in the shape of rice patches.
4. Trophic interactions, measured as the abundance of prey, outweighed the importance of landscape heterogeneity for predators. In contrast, parasitoids responded positively to configurational landscape heterogeneity but were unaffected by prey abundance.
5. *Synthesis and applications*. Our research shows how landscape heterogeneity and trophic interactions have different effects on different functional groups. While predator abundance was solely driven by the availability of prey, all other functional groups in the rice-arthropod community were significantly affected by the

composition and configuration of surrounding landscape features. Landscape management aiming to improve biodiversity and biological control in rice agroecosystems should promote a diversity of land uses and habitat types within 100–300 m radii to reduce the presence of pests. Management practices should also focus on maintaining smaller rice patches and the structural connectivity of rice bunds to enhance populations of the natural enemies of rice pests. Future research should focus on the temporal and spatial manipulation of rice fields to maximize the effects of biological control.

KEYWORDS
arthropods, biological control, farmland biodiversity, landscape heterogeneity, natural enemies, rice, trophic interactions

1 | INTRODUCTION

The importance of landscape heterogeneity in agricultural landscapes for the maintenance of regulatory ecosystem functions, including herbivore regulation, has often been discussed in the scientific literature (Altieri, 1999; Tscharntke, Klein, Kruess, Steffan-Dewenter, & Thies, 2005; Way & Heong, 2009). Several authors suggest that monocultures are associated with declining regulatory services and consequent pest outbreaks (Altieri, 1999). As agroecosystems depend on a variety of ecosystem services, notably biological pest control (Bianchi, Booij, & Tscharntke, 2006; Losey & Vaughan, 2006), there has been an increased focus in recent years on methods such as “conservation biological control”, to maximize agricultural productivity (Bengtsson, Ahnstrom, & Weibull, 2005; Bianchi et al., 2006; Letourneau & Bothwell, 2008). Such approaches aim to enhance natural enemy populations by manipulating the habitat surrounding crops to provide alternative food sources, such as prey, pollen, and nectar, and a refuge from agricultural disturbances and thereby enhance the abundance and functional efficiency of natural enemies (Gurr, Wratten, & Altieri, 2004; Landis, Wratten, & Gurr, 2000).

The biodiversity present in rice landscapes in tropical Asia is often higher than in many natural ecosystems, as many of the species inhabiting rice fields are specialized, open grassland species (Dominik et al., 2017; Schoenly, Justo, Barrion, Harris, & Bottrell, 1998). Nevertheless, the intensification of rice cropping, in combination with the (over)use of insecticides, has led to disruptions in the interactions between herbivores and their natural enemies, resulting in often severe pest outbreaks (Heinrichs, Aquino, Chelliah, Valencia, & Reissig, 1982; Heinrichs & Mochida, 1984; Heong & Schoenly, 1998; Schoenly et al., 1996). Several studies have shown that unsprayed rice fields in less intensive farming systems have fewer pest problems and display little to no crop losses (Horgan et al., 2017; Kenmore, Carino, Perez, Dyck, & Gutierrez, 1984; Way & Heong, 2009). Settele, Biesmeijer, and Bommarco (2008) have called for a switch to conservation biological control (also called ecological engineering; see Gurr et al., 2004) in rice agroecosystems. However, to date only a few studies have focused on the potential benefits of landscape heterogeneity or habitat manipulation for the natural enemies of rice pests (Gurr et al., 2016; Horgan et al., 2017; Lin, You, Yang, & Chen, 2011; Yao, You, Vasseur, Yang, & Zheng, 2012).

Two aspects determine landscape heterogeneity: (a) landscape composition (diversity of landscape features and habitat types) and (b) landscape configuration (number, size, and connectivity of habitat patches; Seppelt et al., 2016). The composition of rice landscapes in tropical Asia is characterized by a mosaic of different habitats that include the rice crop itself, other crops, fallow fields, and natural vegetation. The diversity of habitat patches, neighboring the rice fields, may influence pests, natural enemies, and other biological components of the agroecosystem by modifying the extent of host and prey resources or the quality of microclimatic conditions (Landis et al., 2000; Pickett & Bugg, 1998). Since Asian rice farmers typically own small areas of land (often <2 ha), the configuration of rice landscapes is characterized by a relatively large number of small-sized habitat patches with varying degrees of connectivity. Habitat fragmentation is known to negatively affect natural enemies in temperate agricultural landscapes (i.e. parasitoids: Kruess & Tscharntke, 1994; Thies & Tscharntke, 1999; Tscharntke & Kruess, 1999; predators: Tscharntke & Kruess, 1999). However, rice fields are connected through an extensive network of bunds (levee of terrestrial area surrounding the fields), typically with sparse seminatural vegetation that can potentially offer alternative food resources or refugia to natural enemies (Way & Heong, 2009). The presence of bunds likely facilitates the ability of rice arthropods to move through the rice agroecosystem. For example, egg parasitoids of the genera *Anagrus* and *Oligosita* that cause high mortality of pest planthoppers such as *Nlugen lugens* and *Sogatella furcifera*, occur in wild grasses on rice bunds (Yu, Heong, Hu, & Barrion, 1996). Furthermore, the spider *Pardosa pseudoannulata*, which commonly inhabits bund vegetation, is known to be an early colonizer of newly established rice crops (Sigsgaard, 2000). However, the effects of rice bunds and their functional connectivity on the community composition of rice arthropods are still poorly understood at landscape scales.

In the tropical rice agroecosystems in the Philippines, regional-scale effects (e.g., the effects of elevation as a proxy for climate and other landscape factors) rather than fine-scale landscape heterogeneity explain much of the structure of the arthropod community (Dominik et al., 2017). However, the composition and spatial arrangement of habitat patches can also affect community structure at certain spatial scales (Pickett & Cadenasso, 1995; Roland & Taylor, 1997). Such scale effects are primarily driven by species mobility and thus vary across species (Horner-Devine, Daily, Ehrlich, & Boggs, 2003; Jackson & Fahrig, 2012; Ricketts, 2001).

There is growing evidence that predators and parasitoids are key to regulating herbivore densities in rice agroecosystems (Kenmore et al., 1984; Schoenly et al., 1996; Settle et al., 1996). Attributable to high arthropod diversity in many agro-ecosystems and particularly in tropical rice fields, taxa are often categorized into functional groups to condense information on the huge diversity and provide a research approach to study both food web complexity and community dynamics (Heong, Aquino, & Barrion, 1991, 1992; Settle et al., 1996). Functional groups are a useful descriptor for linking population and ecosystem processes, and for defining the functional differences between herbivores (pests when at high density), natural enemies (predators and parasitoids) and detritivores/tourists (i.e., nonpredatory species that have no direct association with the rice plant but which may be attracted to surrounding habitats; Moran & Southwood, 1982). However, less is known about the way in which trophic interactions have shaped arthropod communities at broader scales, and within the context of landscape heterogeneity. Wiens (2011) suggested that trophic interactions rarely play a role at the landscape scale, or that there are simply too few studies to fully explore the issue.

An increasing number of studies support an idea that the efficiency of natural enemies in regulating herbivores can be enhanced by increasing the structural and compositional diversity of rice-associated habitat (Gurr et al., 2016; Horgan et al., 2016, 2017). Most of this research has been conducted at field and plot scales without regard to the influence of natural vegetation outside and often distant from the experimental plots or fields. This could be an important oversight leading to variability in the success of interventions such as "ecological engineering" that manage rice bunds to enhance natural enemy habitat (e.g., see differences between results from Gurr et al., 2016; Yao et al., 2012; Yu et al., 1996; and those from Horgan et al., 2017 and Sann et al., 2018). Success might depend on the availability of suitable natural vegetation at scales hitherto omitted from research protocols or on the connectivity and form of rice bunds. Therefore, in this study, we compile a unique dataset on rice arthropods sampled from 28 field plots in tropical rice agroecosystems in the Philippines. For the first time, we quantify the heterogeneity of managed rice landscapes surrounding each sampling site based on high-resolution satellite imagery using four independent metrics of landscape composition and configuration. To our knowledge, this is the first study to separate the influences of associated habitat, rice bunds and the trophic composition of rice-associated arthropods on the biocontrol potential of rice landscape. Understanding the influence of such factors in rice is particularly valuable because of architectural restrictions in the design of rice landscapes that require scheduled flooding and draining. We examine the combined effects of landscape heterogeneity and trophic interactions on arthropod communities, particularly the natural enemies, and identify the spatial scales at which these effects are most pronounced. Specifically, we test the following hypotheses:

1. Landscape diversity has positive effects on the abundance and species richness of natural enemies.
2. The configuration of rice landscapes (size of habitat patches and connectivity of rice bunds) has positive effects on the abundance and species richness of natural enemies; and
3. The abundance of natural enemies responds to the abundance of prey.

2 | MATERIALS AND METHODS

2.1 | Study regions

The study was conducted within the project LEGATO (Settele et al., 2015) across three 15 × 15 km regions along an elevation gradient on the island of Luzon in the Philippines. The three regions were: (a) a rice landscape in the hilly lowlands of Laguna Province in southern Luzon (PH_1); (b) an intensively cultivated rice landscape in Nueva Ecija Province (PH_2) situated in central Luzon; and (c) a traditional terraced rice system in the mountainous Ifugao Province located in the north of Luzon (for details, see Dominik et al., 2017; Klotzbücher et al., 2015; Langerwisch, Václavík, von Bloh, Vetter, & Thonicke, 2017). Within each region, 10 "core sites" were selected, resulting in a total of 28 core sites (sampling could not be performed at two core sites in PH_2 because vegetables were planted instead of rice at the time of sampling) (Figure 1). The average distance between the nearest cores sites was ~369 m.

2.2 | Arthropod sampling

The arthropod communities present in the rice fields were sampled during the dry season of 2013 in PH_1 and PH_2 (double cropping is practiced in these regions; however, we only sampled during the dry season) and during the single cropping season of 2014 in PH_3 (which largely corresponded with the Luzon dry season). All samples were collected at the maximum tillering stage of the rice plant (50 days after transplanting) to ensure consistency of sampling; this stage is generally associated with a maximum abundance of arthropods (Heong et al., 1991; Wilby et al., 2006). Since the composition of arthropod communities can change with the development of the rice crop and between cropping seasons (wet and dry seasons: Heong et al., 1991), our analyses focused on the data obtained during the dry season only (January to June).

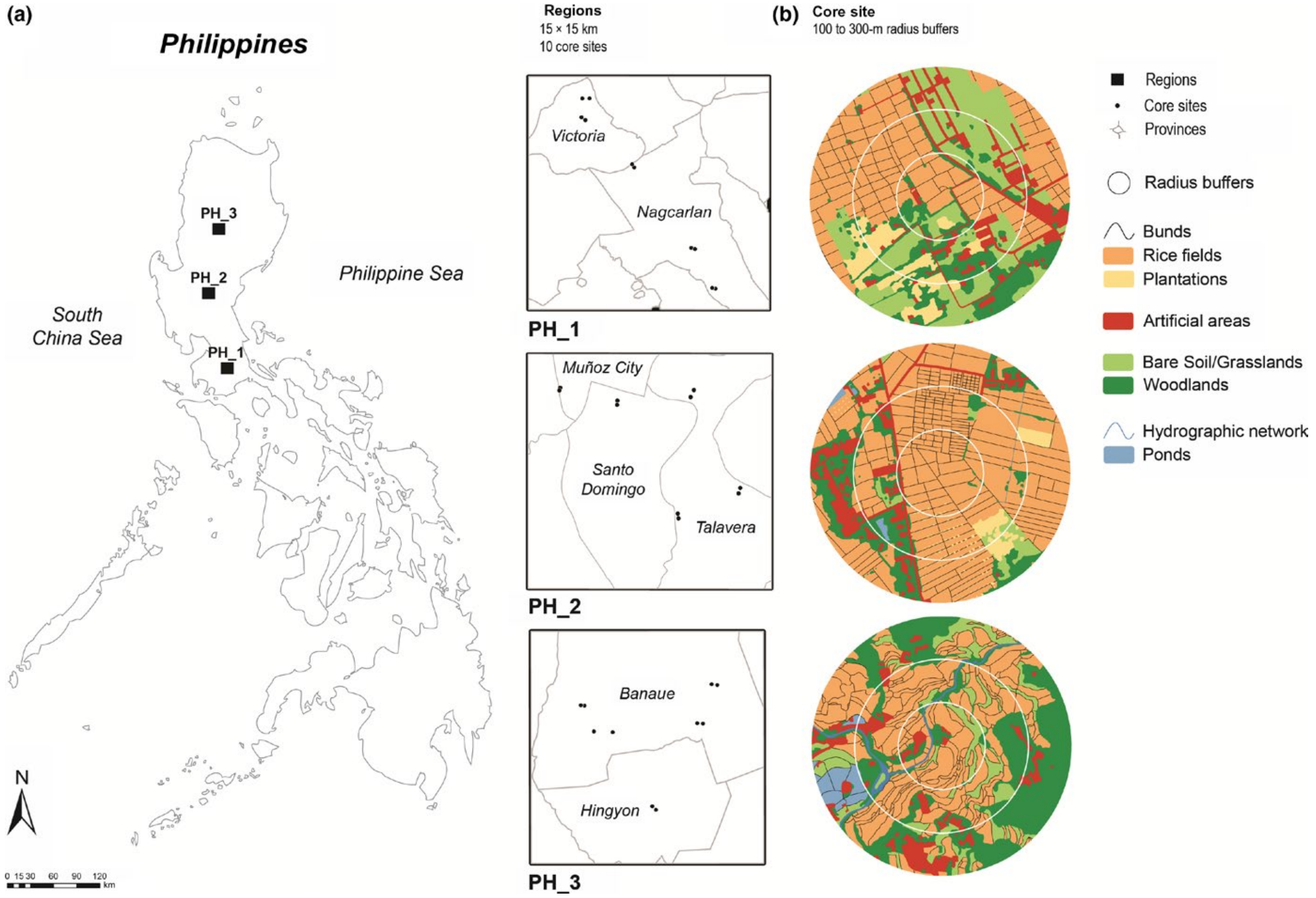

FIGURE 1 Study area on the island of Luzon in the Philippines. (a) Locations of the 15 × 15 km regions in Laguna (PH_1), Nueva Ecija (PH_2) and Ifugao (PH_3). (b) Examples of mapping land cover features within 100, 200 and 300 m radii buffers around core sites [Colour figure can be viewed at wileyonlinelibrary.com]

Arthropods were collected using a modified leaf blower-vacuum (as described by Arida & Heong, 1992). A sampling enclosure of about 1 m side length with a nylon mesh sleeve on the top was used to prevent the escape of mobile invertebrates. The enclosure was placed over four rice hills before suction sampling was performed and captured all arthropods present inside the enclosure. At each core site, five samples were taken at random locations near the centre of the field between 07.00 and 11.00 hr.

Collected arthropods were preserved in 70% ethanol, sorted and identified to species level (or to morphospecies where specimens could not be adequately identified to species level) using a binocular microscope and the taxonomic keys of Barrion and Litsinger (1994). Morphological similarity at the pre-adult stages and quality of the samples limited the identification of arachnids, dipterans and collembolans to family level. Additionally, arthropods were grouped into functional guilds as follows: (a) herbivores; (b) predators; (c) parasitoids; and (d) detritivores and tourists.

2.3 | Mapping and landscape metrics

All landscape features were identified and mapped within a 300-m radius around each sampling site using heads-up digitizing in a geographic information system (ArcGIS 10.3, ESRI) based on high-resolution SPOT-5 DIMAP images (2.5 m). In addition, we collected ground-truth data in June 2014 to verify the photo-interpretation using Collector for ArcGIS (version 9.3, ESRI). We randomly attributed 10 ground-truth locations within each 300 m buffer, verified the land cover in the field and if necessary corrected the digitized maps. Land cover features were classified at a consistent scale of 1:1,000 into eight final categories: rice fields, woodlands, grasslands, artificial areas, plantations, rice bunds, hydrographic network, and ponds (Figure 1b).

To quantify landscape heterogeneity around sampling sites, we calculated four independent metrics of landscape composition and configuration within three buffer distances (100, 200 and 300 m radii) using Fragstats 3.3 (McGarigal & Marks, 1995). As a measure of compositional landscape heterogeneity, we used the Shannon's Diversity Index (SHDI) calculated at the landscape level with all eight land cover categories. Three metrics of configurational landscape heterogeneity focused on the rice landscape and quantified the connectivity, number/size and shape complexity of rice habitat patches. The rice agroecosystem is usually composed of several rice fields (typically 1–3 ha in size) interconnected by a network of terrestrial levees (bunds). Therefore, we calculated the patch cohesion index

(COH) to quantify the structural connectivity of rice bunds and the number of patches (NP) to represent the degree of rice habitat fragmentation (higher numbers representing more fragmented habitat with smaller mean patch size). Finally, we measured the shape complexity of each rice field using the fractal dimension index (FRAC) because the shape of habitat patches may affect the arthropod communities via edge effects, e.g., influencing host finding due to the way that plant odors are emitted from habitat patches (Stanton, 1983). We selected these landscape metrics because (a) they were not correlated with each other, (b) they allowed easy interpretation and (c) they described unique characteristics of landscape heterogeneity (diversity, connectivity, size, and shape).

2.4 | Statistical analyses

The responses of rice-arthropod communities to landscape heterogeneity were analysed using linear mixed-effect models for each response variable and each spatial scale (100, 200, and 300 m). The response variables were (a) the species richness within functional groups, (b) the abundance within functional groups, and (c) the abundance of the most common species (present in at least 20% of the total samples and representing at least 10% of all collected organisms in any sample). The abundance of all arthropods was log-transformed prior to analyses to meet the assumptions of normality (Pinheiro, Bates, DebRoy, Sarkar & R Team, 2014). Since each region has relatively distinct arthropod assemblages and rice management practices (Dominik et al., 2017), subsamples nested within "region" (PH_1, PH_2 and PH_3) were assigned as a random effect. The four metrics of compositional and configurational landscape heterogeneity (i.e. SHDI, NP, COHESION and FRAC) were assigned as fixed effects. Although the main focus of our study was to test the effects of landscape heterogeneity, we included elevation as another predictor because this variable, being a proxy for regional-scale climatic conditions and land-use intensity, has been previously shown to determine the arthropod community composition in our study areas (Dominik et al., 2017). Climate data were obtained from the Advanced Spaceborne Thermal Emission and Reflection Radiometer (ASTER) Global Digital Elevation Model (GDEM) V2 at a 30-m resolution (https://lpdaac.usgs.gov/). A stepwise regression procedure was used together with testing all variable combinations to determine the best-fitting model based on the lowest AIC_c score. The procedure was repeated separately for each response variable and spatial scale.

To account for trophic interactions, additional fixed effects were added to the full models when testing the responses of abundance of individual functional groups. As we expected predator–prey interactions between natural enemies and other functional groups, especially herbivores, the abundance of both predators and parasitoids were added to the model for herbivores and, similarly, the abundance of detritivores/tourists and herbivores were added to the model for predators. Detritivores act as a primary source of food during the early stages of the rice plant for many generalist predators (Gurr et al., 2016; Settele, 1992; Settle et al., 1996). However, interactions between parasitoids and other groups (except for herbivores) have not been documented, thus only the abundance of herbivores was added to the model for parasitoids. Finally, the abundance of predators was included when testing responses in the abundance of detritivores/tourists. Again, the best-fitting models were determined across all spatial scales by selecting the models with the minimal AICc scores.

All statistical analyses were conducted using the *lme* function in the *nlme* package (Pinheiro et al., 2014) in R version 3.1.1 (R Development Core Team, 2016).

3 | RESULTS

In total, we collected 8,547 individuals and identified 113 different arthropod morphospecies across the three study regions. Herbivores accounted for 36.8% of the total arthropods collected and were dominated by the Whitebacked Planthopper (*S. furcifera*), the Brown Planthopper (*N. lugens*), and Green Leafhoppers (*Nephottetix* spp). Predators contributed 26.9% of the total abundance and were mostly represented by dwarf spiders (Linyphiidae), wolf spiders (Lycosidae), long-jawed orb weavers (Tetragnathidae), lady beetles of the genus *Micraspis*, and the mirid bug *Cyrtorhinus lividipennis*. The detritivores/tourists guild represented 29.6% of the total arthropod abundance and was mainly composed of chironomids and collembolans (Isomotidae, Sminthuridae, and Entomidae). Finally, parasitoids accounted for 6.7% of the total abundance and were mainly represented by *Gonatocerus* spp and *Oligosita* spp.

3.1 | Landscape heterogeneity

All best models included the combined effects of compositional or configurational landscape heterogeneity and trophic interactions. However, each functional group and more common species responded differently to landscape heterogeneity (Figure 2). Elevation explained only the abundance of parasitoids ($t = 2.766$, $p = 0.011$) and the predator *C. lividipennis* ($t = 3.278$, $p = 0.003$).

The abundance of herbivores, including the more common species, declined with increasing landscape diversity (SHDI) ($t = -3.383$, $p = 0.003$; Figure 2a). The scale at which herbivores species responded to landscape diversity varied from one species to the next but the best model for herbivores was based on habitat characteristics defined at 300 m (Table 1). Additionally, landscape diversity was negatively correlated with the abundance of Sminthuridae ($t = -2.769$, $p = 0.010$), a family of detritivores. We found no effect of landscape diversity on the abundance or species richness of predators and parasitoids.

In agreement with our second hypothesis, the structural connectivity of the rice bunds (COH) increased the abundance and species richness of most natural enemies, particularly the parasitoids. The abundance ($t = 5.753$, $p = 0.000$) and number of parasitoid species ($t = 3.528$, $p = 0.002$) were strongly correlated with the structural connectivity of rice bunds at the scale of 300 m (Figure 2b). The connectivity of rice bunds also best explained the abundance of *Oligosita* spp ($t = 4.628$,

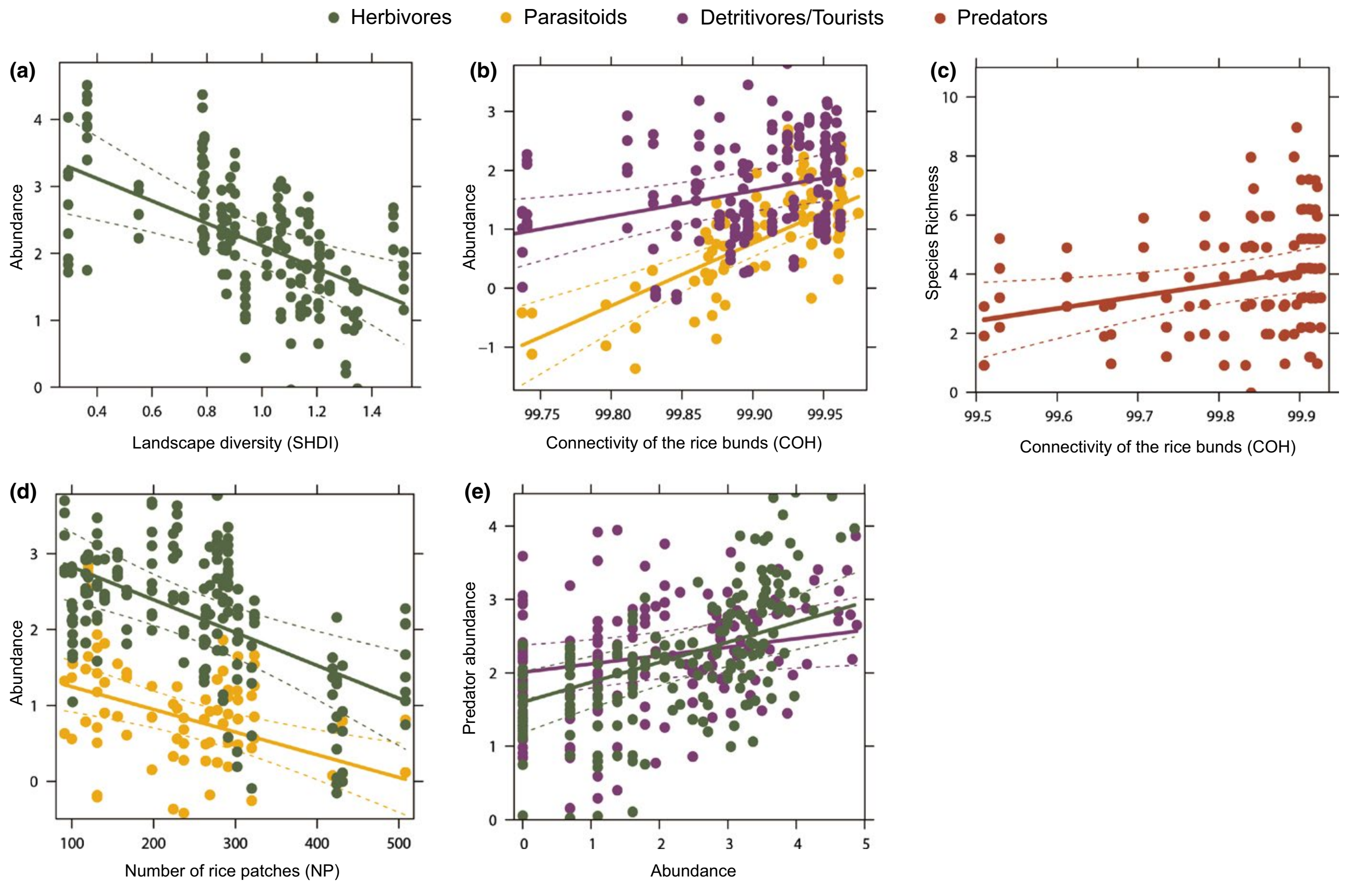

FIGURE 2 Linear mixed effects models representing relationships between (a) landscape diversity (SHDI) and abundance of herbivores, (b) structural connectivity of the rice bunds (COH) and abundance of detritivores/tourists and parasitoids, (c) structural connectivity of the rice bunds (COH) and species 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 [Colour figure can be viewed at wileyonlinelibrary.com]

$p < 0.001$) and *Gonatocerus* spp ($t = 2.458$, $p = 0.022$). The structural connectivity of rice bunds was also the only landscape metric, which explained the species richness of predators. The abundance of long-jawed orb weaver spiders (Tetragnathidae) was also positively correlated with the structural connectivity of rice bunds ($t = 3.596$, $p < 0.002$). The same effect was found for the abundance of detritivores/tourists ($t = 2.762$, $p = 0.011$) and chironomids ($t = 2.360$, $p = 0.027$) (Figure 2b).

The fragmentation of the rice landscape to smaller patches, represented by the number of rice patches (NP), negatively influenced arthropod communities. The abundance of both herbivores ($t = -4.002$, $p < 0.001$) and parasitoids ($t = -3.930$, $p < 0.001$) declined with increasing number of rice patches, measured at 300 m radii (Figure 2c). Similarly, the same pattern emerged with the number of parasitoid species ($t = -2.381$, $p = 0.026$). At the species level, the more common species of all guilds were negatively correlated with the number of rice patches (Table 1). Surprisingly, only the abundance of the predatory Coccinellidae *Micraspis* spp increased significantly with the number of rice patches ($t = 3.299$, $p < 0.003$).

The shape complexity of the rice fields (FRAC) did not influence the total abundance or species richness of the functional groups. However, the shape complexity of the rice fields negatively influenced the abundance of some common species such as spiders from the Linyphiidae family ($t = -2.356$, $p = 0.016$), ladybugs of the genus *Micraspis* ($t = -2.268$, $p = 0.033$), and chironomids ($t = -2.158$, $p = 0.042$). In contrast, the parasitoids *Oligosita* spp. responded positively to the shape complexity of the rice fields ($t = 2.688$, $p = 0.013$).

The scale at which the arthropods responded to landscape heterogeneity varied between functional groups and between species. By comparing the AICs score among the models, the largest scale was constantly favoured when arthropods responded to two or more scales. The detritivores/tourists guild responded to landscape heterogeneity at a smaller scale than the other guilds (200 m and below). Highly mobile arthropods such as parasitoids were typically influenced by landscape heterogeneity at the largest scale (300 m).

3.2 | Trophic interactions

In addition to the effects of landscape heterogeneity, we found significant trophic interactions between herbivores, predators and detritivores/tourists (Table 2). The abundance of predators was highly

TABLE 1 Results of the best-fitting linear mixed-effect models (based on the lowest AIC_c): the effects of elevation (DEM), landscape diversity (SHDI), structural connectivity (COH), fragmentation of the rice landscape (NP), and shape complexity of the rice patches (FRAC) on the abundance (log-transformed) and species richness of functional groups and more common species. The scale at which the effect of landscape heterogeneity was most pronounced (landscape metric entered the best model) is shown as: 100, 200, 300 m, and NA when the scale is undetermined

		Elevation DEM		Landscape diversity SHDI		Connectivity COH		Fragmentation NP		Shape FRAC	
	Scale	*t*	*p*	*t*	*p*	*t*	*p*	*t*	*p*	*t*	*p*
Abundance											
All herbivores	300 m			−3.383	0.003			−4.002	0.001		
Sogatella furcifera	300 m			−3.941	0.001			−3.009	0.006		
Nilaparvata lugens	NA										
Nephotettix spp	200 m			−3.808	0.001						
All predators	NA										
Cyrtorhinus lividipennis	NA	3.278	0.003								
Linyphiidae	300 m									−2.356	0.016
Lycosidae	NA										
Tetragnathidae	300 m					3.596	0.002	−4.394	0		
Micraspis spp	300 m							3.299	0.003	−2.268	0.033
All parasitoids	300 m	2.766	0.011			5.753	0	−3.93	0.001		
Gonatocerus spp	NA					2.458	0.022				
Oligosita spp	300 m					4.628	0	−4.575	0	2.688	0.033
All detritivores	200 m					2.762	0.011				
Chironomidae	200 m					2.36	0.027			−2.158	0.042
Isomotidae	NA										
Sminthuridae	100 m			−2.769	0.01						
Entomidae	NA										
Richness											
All herbivores	300 m							−2.069	0.049		
All predators	100 m					2.42	0.023				
All parasitoids	300 m					3.528	0.002	−2.381	0.026		
All detritivores	NA										

TABLE 2 Results of linear mixed model analyses on the effects of trophic interactions (abundance) between herbivores, predators, parasitoids, and detritivores

	Trophic interactions							
	Herbivores		Predators		Parasitoids		Detritivores	
	t	*p*	*t*	*p*	*t*	*p*	*t*	*p*
Abundance								
All herbivores			3.841	0.000				
All predators	4.587	0.000					2.037	0.043
All parasitoids								
All detritivores			2.379	0.019			2.037	0.043

dependent on the abundance of herbivores ($t = 3.841$, $p < 0.001$). Althoughno effects of landscape composition were found on the abundance of predators, both the abundance of herbivores ($t = 4.587$, $p < 0.001$) and detritivores ($t = 2.037$, $p = 0.043$) explained the abundance of predators (Figure 2d). We found no effects of trophic interaction on the abundance of parasitoids.

4 | DISCUSSION

The responses of arthropod communities to the effects of landscape heterogeneity and trophic interactions greatly differed from one functional group to the next. Although landscape diversity did reduce the abundance of herbivores, it had no effects on the population of natural enemies. The abundance of parasitoids was better explained by the structural connectivity of the rice bunds, rather than by trophic interactions. In contrast, the abundance of predators was solely explained by the availability of prey, showing no significant response to any form of landscape heterogeneity.

4.1 | Landscape heterogeneity

Our analyses did not support our first hypothesis that landscape diversity has a positive effect on the abundance and species richness of the natural enemies of rice herbivores. However, we found that landscape diversity reduced the abundance of the herbivore guild as well as the abundance of two common herbivore genera *Sogatella* and *Nephottetix*. This is potentially explained by the fact that increasing landscape diversity reduces the amount of crop habitat, i.e., the primary area where herbivores thrive. While heterogeneous landscapes with a diversity of habitat types generally increase biodiversity and ecosystem services in agricultural systems, natural noncrop habitats do not always have significant effects on pest control (Sann et al., 2018; Tscharntke et al., 2016). The absence of landscape diversity effects on natural enemy populations may be due to the fact that, even for natural enemies, crops represent more important food and habitat resource than other surrounding habitat types. In our study regions, asynchronous cropping creates a mosaic of cultivated and temporarily unused fields that provide a continuous supply of resources for predators and parasitoids over space and time, helping them to avoid spatial and temporal bottlenecks (Schoenly et al., 2010). In contrast, synchronous cropping could promote more frequent and intense pest outbreaks of green leafhopper (*Nephottetix* spp.) and brown planthopper (*N. lugens*) populations (Sawada, Subroto, Suwardiwijaya, Mustaghfirin, & Kusmayadi, 1992; Widiarta, Suzuki, Sawada, & Nakasuji, 1990). Wilby et al. (2006) showed that local landscape heterogeneity (measured as different crop, crop stage and habitat types) could influence rice-arthropod communities at different stages of the rice plant.

Our observation of strong positive effects of the structural connectivity of bunds on the abundance and species richness of parasitoids is in agreement with Yu et al. (1996), who demonstrated that the egg parasitoids of *Anagrus* spp. and *Oligosita* spp. consumed eggs of nonpest planthoppers in wild grasses on rice bunds during fallow periods when fields were without a rice crop. In our case, the structural connectivity also positively influenced the detritivore/tourist populations. In general, field margins have greater arthropod abundance and diversity than the agricultural fields (Botero-Garcés & Isaacs, 2004; Denys & Tscharntke, 2002) and can provide potential refuge and food resources for flower-visiting, non-pest insects and predatory arthropods (Lagerlöf & Wallin, 1993). The suitability of these field margins as habitat for natural enemies can also depend on the width of the margin and the way margin vegetation is managed. With regard to pest management in rice, new ideas such as ecological engineering aim to manipulate the habitat on rice bunds to enhance biological control (Gurr et al., 2004; Horgan et al., 2016). By increasing the diversity and density of nectar flowering plants along the rice bunds, the fecundity and longevity of many predators and parasitoids potentially increase because they find alternative food resources such as pollen and nectar (Landis et al., 2000; Pickett & Bugg, 1998). The application of ecological engineering at the farm scale has been associated with higher abundances of predators and parasitoids across sites in China, Thailand and Vietnam (Gurr et al., 2016). However, several authors have also indicated that some plants that are commonly used in flowering strips fail to promote natural enemy populations at the field scale (Horgan et al., 2017; Lin et al., 2011; Yao et al., 2012). Additionally, parasitoids were found to be more abundant in rice habitats than in agroforests (Sann et al., 2018). Our results indicate that discrepancies between the results of previous studies could be related to factors such as bund connectivity and field size. We found that the effects of connectivity were most pronounced when measured at the scale of 200–300 m. This suggests that the structural connectivity of bunds surrounding rice fields can potentially contribute to the functional connectivity of highly mobile arthropods such as parasitoids, and that interventions to increase the connectivity of field margins should focus on larger scales, e.g., at least several hundreds of meters.

The arthropod communities in our study strongly responded to the number of rice patches within the defined buffers around sampling sites. Patch area and fragmentation have often been associated with the richness of arthropods (Kruess & Tscharntke, 1994; Steffan-Dewenter, Munzenberg, Burger, Thies, & Tscharntke, 2002). Habitat fragmentation can lead to disruption of the food chain and trophic structure, with predators being generally more vulnerable to fragmentation than their prey. Our study shows that the fragmentation of rice fields negatively influences the richness and abundance of parasitoids but also of herbivores. Specialists such as rice herbivores (e.g., *N. lugens* and *S. furcifera*) are more likely to show a positive density-area relationship in their feeding habitat type than are habitat generalists (i.e., Hambäck et al., 2007). Additionally, parasitoids are often less effective in searching for food resources when in fragmented landscapes (Kruess & Tscharntke, 1994; Tscharntke & Brandl, 2004). However, we did not find the expected negative correlation between fragmentation of the rice landscape and the predator guild. On the contrary, the abundance of a predatory ladybird (*Micraspis* spp) increased with the number of rice patches. Ladybirds of the genus *Micraspis* feed on the eggs, nymphs and adults of a variety of pest insects. They are more abundant during outbreaks of *N. lugens* and during rice flowering when they also feed on rice pollen (Pathak & Khan, 1994). In asynchronous cropping systems, fragmentation of the rice landscape can increase the occurrence of rice crops at different stages (e.g., flowering stage vs. temporarily unused fields), thus smaller rice habitat patches coupled with asynchronous rice fields could enhance mobile predator populations such as *Micraspis* spp. Indeed, it has been shown that arthropods can better colonize rice fields when the rice landscape is a mix of different rice crop stages or interspersed with other crops (Wilby et al., 2006). Mobile predators migrating between fields decreased pest densities more in asynchronous fields than synchronous ones, particularly if predators rapidly colonized newly planted rice fields (Ives & Settle, 1997). For example, the lycosid *P. pseudoannulata*, that inhabits rice bunds during fallow periods, is one of the first natural enemies found in newly established rice crops (Sigsgaard, 2000). In contrast, long-jawed orb-weaver spiders (family Tetragnathidae), which require tall foliage to suspend their webs, cannot rapidly recolonize rice fields (Barrion & Litsinger, 1994). This is also supported by our data where orb-weaver spiders were the only predator species negatively impacted by fragmentation of rice landscape in our study.

Complexity in the shapes of crop patches has rarely been addressed in studies focusing on arthropods. Although patch shape can influence host finding for herbivores (Stanton, 1983), we found no significant relationships between herbivores and shape complexity in our study. On the other hand, the abundance of highly mobile predators and chironomids declined when the shapes of rice patches increased in complexity. As patches become more irregular, the perimeter-area relation of the patches changes considerably. For example, Grez and Prado (2000) showed that coccinellids in Chile emigrated less from square patches (simple shape with a low perimeter-area ratio) than rectangular patches (more complex shape with a high perimeter-area ratio) of wild cabbages. It was suggested that coccinellids are more likely to emigrate and abandon the more complex shapes because of the accessibility of alternative habitats and prey. In contrast, in our study the parasitoids from the genus *Oligosita* were more abundant in complex patch shapes where the perimeter-area ratio was higher, suggesting that the edge effect of field margins is important for parasitoids in rice fields. Such a factor could also determine the success of interventions such as ecological engineering.

The scale at which arthropods responded best to the landscape metrics varied among functional groups and species and partly reflected their dispersal abilities. Detritivores/tourists and predator guilds mostly live at the base of the rice plants and are either wingless (collembolans, spiders) or limited in flight (chironomids). Thus, the scale at which they responded (100 and 200 m) is expected to be lower than for highly mobile flying arthropods such as parasitoids (300 m). Some rice herbivores such as delphacids exhibit a physical dimorphism with a fully winged “macropterous” form and a truncate-winged “brachypterous” form (Heong & Hardy, 2009). The macropterous delphacids can colonize and disperse to multiple habitat patches and thus could be the reason why herbivores responded to the landscape metrics at a larger scale (300 m). While the long-jawed orb-weaver spider (Tetragnathidae) has low mobility, it still responded to the number of patches at a broad scale (300 m). However, a buffer of 100 m might not be enough to capture the fragmentation of the rice landscape, and thus, arthropods may respond to this landscape metric at broader scales only.

4.2 | Trophic interactions

The predator guild showed a strong numerical response to prey density. The abundances of predators were associated with a higher abundance of both herbivores and detritivores/tourists. In our study, spiders represented most of the predator guild and have been noted to respond numerically to prey density (Kenmore et al., 1984; Riechert & Lockley, 1984). In the early stages of the rice plant, when the abundance of herbivores is low, detritivores act as an alternative prey for generalist predators (Gurr et al., 2016; Settle et al., 1996). Kenmore et al. (1984) suggested that a greater availability of food for predators could lead to an increase in the predators’ fitness leading to more offspring, lower competition, and higher survival of smaller individuals. The absence of a density-dependent relationship between parasitoids and herbivores can be explained by the sampling methods we used in our study. In a previous study, Horgan et al. (2017) showed that despite the lack of numerical response of parasitoids to herbivores in rice fields, egg parasitism was still density-dependent. Our sampling method did not measure egg abundance as a determinant of parasitoid abundance (i.e., parasitoid individuals remaining in larval stages inside the eggs or larvae of herbivores), and thus parasitoids sampled at the adult life stage may not have responded to prey the same way as generalist predators. Indeed, predator populations were largely driven by the availability of prey, likely masking any effects of landscape heterogeneity.

4.3 | Synthesis and applications

Our study shows, for the first time, that the combined effects of landscape heterogeneity and trophic interactions shape arthropod communities in rice agroecosystems. Fragmentation of the rice-production habitat is expected to increase production costs particularly since it constrains mechanization (Kawasaki, 2010); however, it can be beneficial for farmers, as it limits the risks of pest outbreaks, particularly if the production costs are not considerably higher than the ecosystem services it provides (i.e., weed and herbivore control). Our study provides evidence that increasing the landscape diversity surrounding rice fields and increasing the number of rice patches can result in lower herbivore abundance. The bunds interconnecting rice fields are an important feature for parasitoids and predators, and more studies should focus on the potential functional connectivity of bunds in enhancing natural enemies particularly as a factor in the success of interventions such as crop diversification and ecological engineering. Manipulating the landscape to create a mosaic of rice fields with different temporal and spatial compositions and configurations could also provide natural enemies with a continuous availability of food. Arthropods with low dispersal ability such as spiders may benefit from the high availability of prey in the neighboring patches at a small scale, while flying arthropods with high dispersal ability such as parasitoids may benefit from the configuration of the landscape at larger scales. Based on these findings we recommend that landscape management to improve biodiversity and biological pest control in rice agroecosystems should promote a diversity of land uses and habitat types within at least 100–300 m radii, maintain smaller rice patches and enhance the structural connectivity of rice bunds.

Our study was conducted in a real agricultural setting in which land management factors, such as pesticide input or cropping synchrony, were not controlled. Management practices and to a larger extent the use of insecticides can potentially disrupt the predator–prey relationships and the food web structure, ultimately leading to the loss of arthropod biodiversity and the reduction in the agroecosystem resilience to pest outbreaks (Heong et al., 1991; Horgan & Crisol, 2013; Kenmore et al., 1984; Way & Heong, 2009). In a previous study (Dominik et al., 2017), we have shown that management effects are potentially important in determining the arthropod composition in our study areas but that they vary between regions, while being relatively homogeneous within regions. Although these regional-scale effects cannot be fully disentangled from the effects of landscape heterogeneity, in this study we indirectly accounted for them by the nested design of our analyses. To further unravel the effects of landscape heterogeneity on arthropod communities, future research should directly address management practices and land-use intensity as additional factors potentially shaping rice arthropod communities. In addition, future research should focus on the effects of temporal and spatial manipulation of the rice landscape, and on the potential benefits of coupling small rice patches with large ones to better understand the effects of fragmentation in rice agroecosystems.

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AUTHORS’ CONTRIBUTIONS

C.D., R.S., T.V., and J.S. conceived the idea and designed methodology; C.D. and F.G.H. collected the data; C.D. analysed the data; C.D. and T.V. led the writing of the manuscript. All authors contributed critically to the drafts and gave final approval for publication.

DATA ACCESSIBILITY

Data available via the Dryad Digital Repository https://doi.org/10.5061/dryad.6mv5372 (Dominik, Seppelt, Horgan, Settele, & Václavík, 2018).

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Appendix 9

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SYNTHESIS AND REVIEW

Focus on cross-scale feedbacks in global sustainable land management

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1. Introduction

Human land-use activities have transformed most of the Earth's land surface (Foley *et al* 2005, Ellis 2011, Gauthier *et al* 2015). While land-use activities differ in many ways across the world, their combined impact is becoming a force of global importance. Consequently, sustainable land management has been identified as a key lever for achieving global sustainability. For example, six out of 17 sustainable development goals (SDGs), adopted in the United Nations 2030 Agenda for Sustainable Development, relate directly to land management: (i) land management is key for providing goods and services for humankind relating to 'zero hunger' (SDG 2); (ii) land management is responsible for 20%–40% of greenhouse gas (GHG) emissions relating to 'climate action' (SDG 13), and (iii) land management is a major driver of biodiversity loss relating to 'life of land' (SDG 15). Indirectly, land management affects 'affordable clean energy' (SDG 7) and 'sustainable cities and communities' (SDG 11).

A growing human population, associated with increasing consumption rates and demands on commodities, requires a true paradigm shift regarding the management of the land for long-term sustainability. At the same time, we are witnessing a progressive scarcity of available productive land, and the production peak of many renewable resources has already been passed (Lambin and Meyfroidt 2011, Seppelt *et al* 2014). These demands and the limits to supply underlie the many linkages between the different social, economic and ecological goals and targets that are being charted out by Agenda 2030 (Geijzendorffer *et al* 2017). Pathways to some goals are synergistic, while others present trade-offs for their mutual achievement. For example, an increase of provisioning goods and services from ecosystems, such as food and fibre, could be achieved through further intensification of land use (Mauser *et al* 2015), which might lead to an increased loss of biodiversity (Gerstner *et al* 2014, Stein *et al* 2014, Newbold *et al* 2015) but also result in higher GHG emission through higher energy use and fertilizer application. At the same time, biodiversity has to be maintained for many societal objectives including its potential to support ecosystem functions such as pollination (Cardinale *et al* 2012, Seppelt *et al* 2016). A significant reduction of GHG emissions through large-scale deployment of new biofuels is in conflict with the production of food or conservation of natural habitats for biodiversity or carbon storage. The specific nature of the conflicts and synergies between these different objectives strongly depends on the local land system and the environmental, socio-economic and cultural context in which this land system is operating. Thus, achieving one SDG might compromise others (Pradhan *et al* 2017) and trade-offs on various scales need to be expected, which can be moderated by appropriate land management.

Whilst place-based research provides essential knowledge on the biophysical and socio-economic boundaries of land use, its findings are naturally contingent upon the specific geographical context and rarely account for offsite effects. The conversion of a conventional agricultural system at one location to organic farming may have positive impacts on local sustainability, but it may, due to lower production, displace some impacts to other locations that need to compensate for the loss of production. On the other hand, many land use drivers such as climate change, population growth or consumption patterns are well captured at the global scale, but there are significant uncertainties about how they interact with local conditions. Both regional and global studies on food production rarely account for these tight links and interactions between socio-economic and biophysical processes. These uncertainties and incongruences in spatial scales prevent effective integration, synthesis and transferability of findings from research to sustainable land management.

Against this background, here we review and synthesize the contributions of the focus collection on 'Cross-scale Feedbacks in Global Sustainable Land Management', which collates papers that investigate the links between global change processes and local realities through, e.g., integration of local and global drivers impacting economic and biophysical processes or assessing the transferability or up-scaling of findings from place-based research.

2. Synthesis: emerging topics in sustainable land management and land systems research

The articles in this focus issue illustrate new approaches to investigate global and regional land systems, and identify key research frontiers important for sustainable land management across scales to achieve the SDGs. Three major clusters of research frontiers have been identified: (1) new frameworks to understand cross-scale dynamics of land-use systems, (2) synthesis of place-based research, and (3) addressing future perspectives of land use by development of consistent scenarios.

2.1. New frameworks to understand cross-scale dynamics of land-use systems

Land management dynamics are seldom just local or place-specific anymore, but are influenced by multiple global drivers with complex connections to other places. Improving our understanding of these different cross-scale dynamics in diverse land-use systems is critical. Dorninger *et al* (2017) conceptualize 'human-nature connectedness' as a new methodological framework that can be applied in any region of the world to assess how closely connected people are to their regional ecosystems. The authors identify two key mechanisms that disconnect humans from nature on a regional scale: (1) the flow of external non-renewable inputs into the land-use system and (2) teleconnections with distant systems. While these mechanisms allow for greater regional resource use, they pose challenges for sustainability through waste generation, depletion of non-renewable resources and environmental burdens shifted to distant regions.

The topic of environmental burdens is elaborated by Pascual *et al* (2017), who argue for a better recognition of the distant, diffuse and delayed impacts that land management often has on biodiversity and ecosystem services. They define these impacts as 'off-stage ecosystem service burdens' and identify four typical pathways based on biodiversity conservation policies, and the management of provisioning, regulating and cultural services. The authors advocate for their incorporation in land management decisions and ecosystem service assessments such as those conducted by the Intergovernmental Science-Policy Platform on Biodiversity and Ecosystem Services.

Finally, Sietz *et al* (2017) apply the emerging approach of 'archetype analysis' and assess vulnerability in African drylands to environmental change. A cluster analysis reveals archetypical patterns of how vulnerable farming systems are to land degradation and support understanding the heterogeneity of vulnerability determinants (e.g. water availability, agro-ecological potential or population pressure) across sub-Saharan Africa. Importantly, their spatially explicit framework offers the opportunity to evaluate a specific region's potentials and challenges in its wider context across nested scales.

2.2. Synthesis of place-based research results

While new conceptual and analytical frameworks such as the above provide guidance in designing specific analysis and provide suggestions for similarities between case studies, a general methodology on the transferability of place-based research is unresolved and defines the second emerging topic. Three studies focus on the synthesis of data and local case studies on sustainable land management, highlighting the need for generalization and transferability of findings. Hermans-Neumann *et al* (2016) analyse the drivers of changes in tropical forest products using a standardized, pan-tropical dataset of more than 200 villages with forest access. Their analysis shows that forest resources (e.g. timber, fuel wood and food) declined over the last five years, though with marked differences across continents. The strongest degradation of forest resources occurred in places with both growing resource use and immigration.

Similarly, Carter *et al* (2017) synthesize comprehensive data on large-scale land acquisition (LSLA) to reveal that land available for agriculture, accessibility and political stability are the main factors that explain whether a country will be targeted for LSLA. The synthesis of such comprehensive datasets allows for globally comparative analyses that go beyond case studies in terms of generalizable conclusions and transferability of findings.

The issue of transferability is specifically addressed by Václavík *et al* (2016) who build on a previously developed concept of land system archetypes (Václavík *et al* 2013, Levers *et al* 2018) to investigate potential transferability of regional case studies that focus on land management and ecosystem services across four continents. The proposed method is offered as a blueprint for large research frameworks that need to assess the relevance and representativeness of place-based research for other geographical areas and to identify possible gaps in research efforts.

2.3. Future perspectives and new integrated scenarios

Finally, the third emerging topic deals with potential future developments of land management based on scenarios which capture the diversity of land systems. Scenarios of land management need to consider that land is a limited resource which can be used to produce food and fibre or to maintain non-provisioning ecosystem services but that trade-offs exist in the decisions on how to manage land (Titeux *et al* 2017). Modelling approaches that integrate the interplay of biophysical and socio-economic factors in scenarios of global or regional change are promising tools to study future land-use impacts and trade-offs. Delzeit *et al* (2018) provide a set of scenarios of global drivers until 2030 that can be used consistently in a range of regional and local case studies of land use. The impacts of biofuel policies, dietary patterns, cropland expansion and productivity changes on agricultural markets are investigated in a modelling framework that couples an economic model with a crop growth model.

One of these global scenarios, together with regionally-tailored land-use and climate change scenarios, is applied by Langerwisch *et al* (2018) who quantify the combined effects of land-use and climate change on four ecosystem services in rice production regions in Southeast Asia. Here, the vegetation and hydrology model LPJmL shows clear trade-offs in the future provision of ecosystem services, but also the potential of land management to partially offset the negative impacts of climate change on rice production, carbon storage and sequestration. Following a similar framework, Gutsch *et al* (2018) quantify the effects of alternative land management scenarios and climate impacts on forest variables indicating ecosystem services related to timber, habitat, water and carbon. Again, the combination of modelling tools applied under scenarios of future change allows one to better balance the trade-offs between ecosystem services and provides the base for future forest management optimization at the regional and national scale.

3. Outlook: guiding questions of the emerging topics

Obviously, a focus collection of publications such as this cannot fully cover the complex topic of sustainable land management in a comprehensive or exhaustive manner. Global land management is characterized by a diverse set of key challenges. These range from sustainable resource appropriation, the preservation of biodiversity and ecosystem functioning, human well-being, equity and so forth, as comprehensively covered by the SDGs, or as illustrated by figure 1. Based on the emerging topics identified by and discussed in the contributions of this focus collection we can collate key questions, which serve for stimulation as well as for guidance of future research directions; cf Box 1.

There is a predominant paradigm that an improved understanding of the system of interest, here land systems, is key to improve decision making. However, despite a significant increase in our understanding of land system dynamics over the past two decades, the uptake and integration of scientific knowledge into decision-making processes remains limited (Kirchhoff *et al* 2013). This is because decision-making only partly relies on well-established scientific knowledge. Of equal importance are the underlying value systems of the involved decision-makers, beneficiary and stakeholders as well as the governance system and power structures in which decision can be taken, namely rules, values and knowledge, cf Gorddard *et al* (2016). Consequently, a simplistic focus on generating more understanding of land system dynamics will likely in itself be insufficient to foster sustainable land management.

Moving towards alternative approaches to science-policy interactions, such as co-production (Mauser *et al* 2013), could increase the relevance and usability of land-use science for society and decision-making. With respect to global land *governance*, new emerging processes such as large-scale land acquisition or spill-off and offsite effects (Seppelt *et al* 2011, Carter *et al* 2017, Pascual *et al* 2017) pose challenges to land management which is mostly implemented through law, rule or incentives at the local to regional scale. Surprisingly, large-scale land acquisitions are not an issue in global-scale agro-economic models (Debonne *et al* 2018). A proper representation of changes in farming structure, including their underlying social, economic and political drivers, is important to be able to analyse the environmental, economic and social impacts of such changes and the ways in which these new modes of land governance impact on the relations between global and local processes. The limitation of the available land surface and the limitation of its goods and services produced simply suggests that novel ideas to govern land as global commons are required (Seppelt *et al* 2014, Creutzig 2017).

This focus collection also contrasts two different conceptual approaches to the *synthesis of place-based research results*: (a) global-scale analysis and modelling, that builds on the basic assumption to fully capture global processes related to land use and (b) linkage of a variety of locations studied as different case studies. While global trade models are limited with respect to spatial scale but also with respect to the commodities captured, a similar limitation holds for the synthesis of place-based results. For the latter, concepts like

Figure 1. The diverse facets of global sustainable management of land systems (artist: M. Volk). The main task of balancing different trade-offs, such as between various SDGs, by the artistic guy in the center of the picture, mostly model-based (cf sign), has to cope with various challenges (smaller cartoons in different world regions): deforestation, invasive species (e.g. South America), water scarcity, high-tech agriculture, global trade (e.g. North America); renewable energies and bio-based economies, global trade (e.g. Europe), large-scale land acquisitions, mining and resources extraction (e.g. Africa), urbanization (e.g. East Asia), mining and resources extraction, invasive species (e.g. Australia).

tele-coupling, offsite effects or spill-over emerge quite logically (Seppelt *et al* 2011, Liu *et al* 2015, Pascual *et al* 2017). Although tele-coupling is well conceptualized, operationalization in research methods is still challenging. The literature is full of local case study evidence of potential impacts of emerging value chains and the role of market-based commodities and tele-coupled land management (Lenzen *et al* 2012). However, these local insights are poorly coupled to larger scale assessments and life cycle analysis where impacts are only considered ‘on average’ ignoring the importance of local land systems as determinants of the impacts of these global relations.

For developing future perspectives on sustainable land management based on scenario approaches a better integration of feedbacks is needed, cf Delzeit *et al* (2018). Gaps still relate to understating land use intensity, landscape homogenization and the feedback between landscapes, agricultural production and biodiversity of managed landscapes (Seppelt *et al* 2016, Verburg *et al* 2016), specifically as humans shape emerging or novel ecosystems. Two understudied feedbacks pose major challenges for future global land systems research. First, the mutual dependence between biodiversity and agricultural production is understudied in global studies and models: biodiversity is negatively affected through land-use intensification, which is mostly applied to boost yields. Maintaining yields on a high level, however, requires various facets of biodiversity for support of important ecosystem functions such as nutrient cycling, biocontrol or pollination (Seppelt *et al* 2016). Research for embedding these feedbacks quantitatively in global-scale models is advancing and could become crucial for global assessments in the near future (Rosa *et al* 2017).

Second, the feedback between commodity production and consumption are also understudied. Usually demand trajectories are predefined, such as by predefined scenarions, e.g. Delzeit *et al* (2018). Jevons paradox-like, rebound phenomena, which denote the increasing demand for a resource after establishing a more resource efficient production method (Alcott 2005), are mostly neglected in today’s scenarios analysis. This might hamper understanding of rebound effects and probably leads to overly positive estimates on certain scenarios.

Given the limited land resources available and multiple competing claims on these resources, sustainable land management should also include

Box 1. Outstanding questions of the emerging question in sustainable land management.

Enhancing understanding of the diversity of land systems
- Are the correct drivers addressed for investigating solutions on sustainable land management, considering the knowledge, values and rules define the decision context?
- How to capture countries activities and characteristics properly to account for emerging issues such as large-scale land acquisition, or long-distance externalization of effects within global agro-economic models?
- What are the options to govern land as global commons?

Synthesis of place-based research results
- Which are the next steps to enable global agro-economic models to address a larger set of commodities, different land-holding systems, capture nutrient cycling and provide sufficient information on food security question on a finger spatial resolution?
- How can the tele-coupling concept be operationalized in research to better underpin and embed life cycle analysis in global relations?
- Which data gaps should be closed to better account for local variations in the socio-economic context of sustainable land management?

Future perspectives and new scenarios
- How to implement the mutual feedback of biodiversity and agricultural production in today's global model system estimation global agricultural yields and estimate optimum intensification levels?
- To what extent do concepts like sustainable intensification that claim to have synergies between SDGs really have potential, what are the trade-offs hidden in these systems and in what local context are such concepts applicable?
- How can integrated scenarios capture the links between production and consumption, rebound effects and Jevons paradox?

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sustainable consumption (Scherer and Verburg 2017). While sustainable consumption is also one of the SDGs it is hardly related to land management. Recent work of Alexander *et al* (2016) shows the strong impacts of consumption and value-chain losses on agricultural production, indicating the potential reduction on land resources that can be achieved through improved consumption and value-chain management.

This focus collection provides several contributions in the fields of land system science to the development of concepts, models and tools for sustainable land management. To advance beyond the current state of the art, future research directions need to address a diversity of topical challenges such as poverty reduction, large-scale land acquisition, global feedbacks of agricultural production and biodiversity. While research questions can be developed easily, we acknowledge that further research needs shall not hamper action with respect to lowering pressure on the environment by all possible means. Research needs are no excuse for inaction (Voinov *et al* 2014).

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Appendix 10

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ARTICLE

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Global impacts of future cropland expansion and intensification on agricultural markets and biodiversity

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With rising demand for biomass, cropland expansion and intensification represent the main strategies to boost agricultural production, but are also major drivers of biodiversity decline. We investigate the consequences of attaining equal global production gains by 2030, either by cropland expansion or intensification, and analyse their impacts on agricultural markets and biodiversity. We find that both scenarios lead to lower crop prices across the world, even in regions where production decreases. Cropland expansion mostly affects biodiversity hotspots in Central and South America, while cropland intensification threatens biodiversity especially in Sub-Saharan Africa, India and China. Our results suggest that production gains will occur at the costs of biodiversity predominantly in developing tropical regions, while Europe and North America benefit from lower world market prices without putting their own biodiversity at risk. By identifying hotspots of potential future conflicts, we demonstrate where conservation prioritization is needed to balance agricultural production with conservation goals.

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For thousands of years, humans have cultivated the planet to satisfy their needs for food, fibre and energy. Today, farmlands dominate 38% of the global land surface[1] and almost 30% of global net primary production is appropriated for human use[2]. The pace of farmland production growth is unlikely to continue[3], but the demand for agricultural commodities is projected to increase inexorably (70–100% by 2050)[4,5]. Since the focus on agricultural production is motivated also by income generation and economic growth, high pressure on farming systems will continue in the next decades[6–8].

As a result, agriculture is likely to remain the primary driver of global biodiversity loss, because both strategies to increase production, namely cropland expansion and intensification, pose major threats to many common as well as IUCN red-listed species[9,10]. While cropland expansion into uncultivated areas threatens biodiversity mainly through the loss and fragmentation of natural habitat[11,12], the negative effects of cropland intensification may be less pronounced[13]. There is clear evidence, however, that land-use intensification threatens multiple taxa of primarily farmland species due to habitat homogenisation[14,15], irrigation[16] and high inputs of agro-chemicals[17,18], such as fertilisers and pesticides. Therefore, meeting future biomass demands while, at the same time, safeguarding remaining ecosystems and biodiversity is a critical challenge we face in the 21st century[19] (Sustainable Development Goals 2, 12 and 15[20]).

Recent advances in data availability[21–23] and spatially explicit modelling of land systems[24–26] improved our ability to assess future agricultural impacts. General solutions to cope with the increasing demand for agricultural resources have been proposed[27,28] but the spatial relationship between different farming strategies and biodiversity patterns have been understudied. Although cropland expansion and intensification often occur simultaneously, recent studies evaluated only one aspect separately or did not separate intensification from expansion processes[29–33]. Often a limited set of production metrics was used (e.g. yields[34,35]) or biophysical constraints of farmland production were considered but socio–economic drivers were ignored or vice versa[36,37]. Changes in agricultural productivity are addressed in some scenario studies feeding yield changes into partial or general equilibrium models[38–40], but feedbacks from the economic model to biophysical models are neglected. Thus, emerging trade-offs have not yet been addressed using comparable scenarios that integrate biophysical and socio–economic drivers of crop production[12,34,41–44]. Therefore, integrated approaches are required that

(i) utilise comparable scenarios of both cropland expansion and intensification,
(ii) account for spatial information on biophysical constraints as well as socio–economic drivers of agricultural production,
(iii) capture repercussions of changes in supply and demand on regional and global markets, and
(iv) estimate how different farming strategies and their impacts on biodiversity play out across space.

This is crucial to assess the feasibility of achieving desired agricultural pathways and minimise their impact on areas with the highest conservation value.

Here we capture feedbacks between biophysical and socio–economic drivers of land-use change as well as interactions with biodiversity. We examine global trade-offs between agricultural markets and global biodiversity that future farmland production may impose (Fig. 1). First, we combine two established approaches from previous work of the authors[6,29], 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 (see Supplementary Notes 1, 2, 3). These crops represent 73% of global cropland area and crop production[45] and cover the most important staple and energy crops, to also capture trends in political support of biofuels.

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. Second, we examine the impact of cropland expansion and intensification on agricultural markets (Supplementary Note 4). To do so, we apply 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. These are compared to a reference scenario that carries forward current trends in population growth, gross domestic product and trade policies[46]. The cropland expansion scenario allows additional 7.3 million km^2 of land to be available for crop production in areas with the highest 10% of global expansion potential. Comparably, the cropland intensification scenario allows closing yield gaps on 10% of land with the highest global intensification potential, up to the level that both scenarios leads to equivalent global production gains (Supplementary Note 1). Finally, we use global range maps for 19,978 vertebrate species to examine the spatial concordance between patterns of global biodiversity and potentials for near-future cropland expansion and intensification (see Supplementary Notes 5, 6). Our goal is to (1) quantify the relative differences in the impact of alternative global farming strategies (cropland expansion vs. intensification) on crop yields, prices, trade and consumption, and to (2) identify hotspots of potential future conflicts between cropland expansion, intensification and biodiversity.

Results

Impacts on agricultural markets. Both farming strategies resulted in additional 19% of global crop production compared to the reference scenario. While in the expansion scenario, an area of 7.3 million km^2 is additionally used for crop production, an area of 1.5 million km^2 is intensified in the intensification scenario. Both strategies had different impacts on considered geographical regions. When compared to the reference scenario in 2030, the changes in production under the cropland expansion mirrored the relative changes in cropland expansion area (Supplementary Fig. 4): crop production increased most in South and Central America (+146%) and in Australia/New Zealand (+78%) (Fig. 2). Due to the increase in supply in agricultural markets, crop prices fell in all regions, including those regions where domestic production decreased (e.g. EU, USA, Russia). The EU turned from a net-exporter to a net-importer, while the net-importer Russia increased imports due to lower world market prices (Supplementary Fig. 15).

Cropland intensification caused the strongest increases in production in Sub-Saharan Africa (+78%), India (+68 %), and Former Soviet Union (+63%) (Fig. 2). Crop prices dropped strongest in regions with high total intensification potentials and high shares of top 10% areas on total land endowment such as Sub-Saharan Africa and India (Supplementary Fig. 8), while others (e.g. EU and Middle East and Northern Africa) also benefited from lower world market prices.

The comparison of the expansion and intensification scenarios showed an increase in crop production, e.g. in Sub-Saharan Africa and Australia, but it also showed contradicting impacts on several regions: crop production increased significantly in Central and

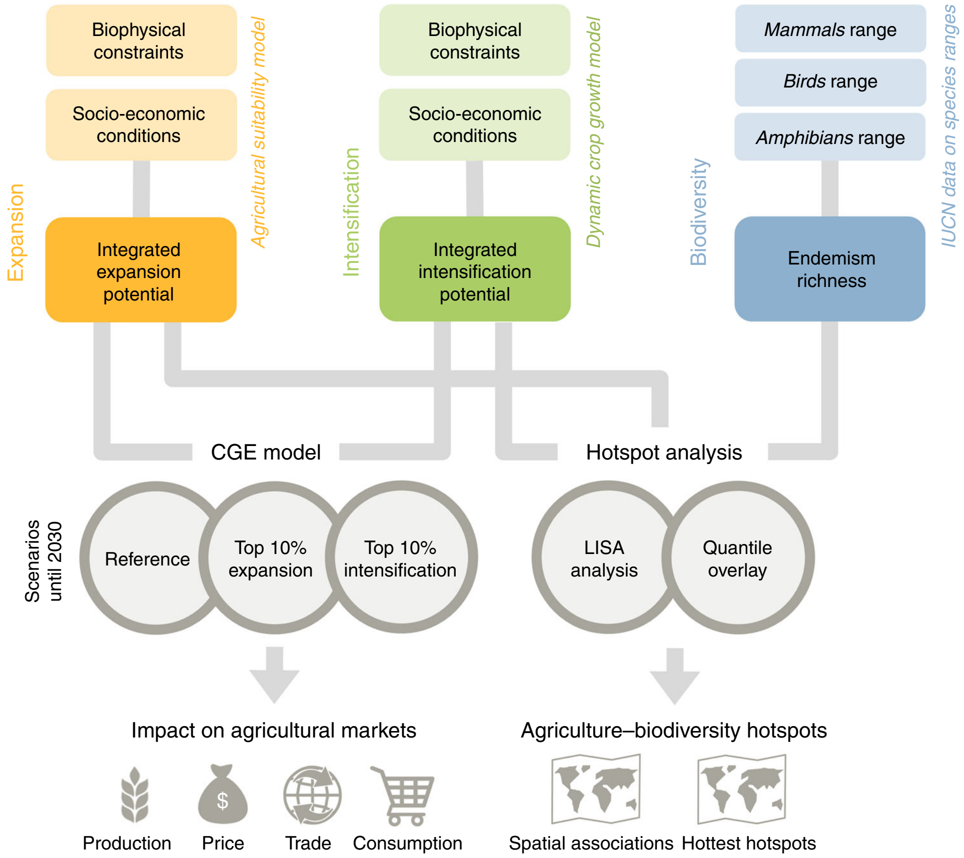

Fig. 1 Overview of the study design. The study is based on three sources of data on global cropland expansion, intensification and biodiversity. Both maps of cropland expansion potential and intensification potential are simulated for 17 major agricultural crops at 30 arc sec resolution and integrate information on biophysical constraints (e.g. topography, soil quality, climate change) and socio-economic conditions (e.g. population growth, consumption patterns). The integrated cropland expansion potential is developed by a model of near-future agricultural suitability, while the integrated cropland intensification potential is developed by a dynamic crop growth model. A computable general equilibrium (CGE) model of the world economy, applied to two scenarios of cropland expansion and intensification until 2030, quantifies the impact on agricultural markets in terms of crop production, price, trade and consumption. We use a reference scenario up to 2030 for reference that carries forward current trends in population growth, gross domestic product and trade policies. Endemism richness integrates IUCN range maps of 19,978 species of mammals, birds and amphibians into a global biodiversity metric aggregated at 55-km resolution of an equal-area grid. This metric combines species richness with a measure of endemism (i.e. the range sizes of species within an assemblage) and thus indicates the relative importance of a site for conservation. Hotspot analysis, using Local Indicator of Spatial Association (LISA) and quantile overlay, identifies hotspots where global biodiversity is most affected by near-future cropland expansion and intensification

South American countries under the cropland expansion scenario, while crop production decreased under the intensification scenario. The opposite effect appeared, e.g. in India and China. While the intensification scenario caused crop production in these regions to increase by 68 and 5%, respectively, the low expansion potentials caused crop production to decrease by 2 and 3% under the expansion scenario. Notably, India was a net-importer of crops under the expansion scenario, while it was a net-exporter under the intensification scenario (Supplementary Fig. 15).

One would expect that given relatively large cropland intensification potentials (Supplementary Fig. 8), Sub-Saharan Africa would increase crop consumption more than, e.g. China with lower cropland intensification potentials. However, with a stronger economic growth compared to Sub-Saharan Africa, China increased its net imports of crops such that food consumption increased stronger than domestic production (Supplementary Figs. 15, 16). Hence, the impacts of farming strategies on agricultural markets did not only depend on the changes in land productivity or land endowment, but were a result from market mechanisms, since the economies compete under flexible prices on global markets.

Agriculture–biodiversity hotspots. Both farming strategies resulted in equal global production gains of 19% more crop yields than the reference scenario (Fig. 2) but differed substantially in their impact on biodiversity. To understand how cropland expansion, intensification and biodiversity are interlinked, we first examined statistically significant spatial associations between gradients of estimated agricultural potentials in 2030 and endemism richness for expansion and intensification separately (Fig. 3).

The hotspot regions where high biodiversity will be most threatened by cropland expansion or intensification in 2030 were found overwhelmingly in the tropics, with cropland expansion affecting larger areas than cropland intensification (significant hotspots covering 14 and 8% of the terrestrial ecosystems, respectively). Biodiversity hotspots under cropland expansion pressure occurred 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 (Fig. 3a). The cropland intensification pressure on biodiversity was generally less pronounced, especially in Latin America, but included regions in Sub-Saharan Africa, India,

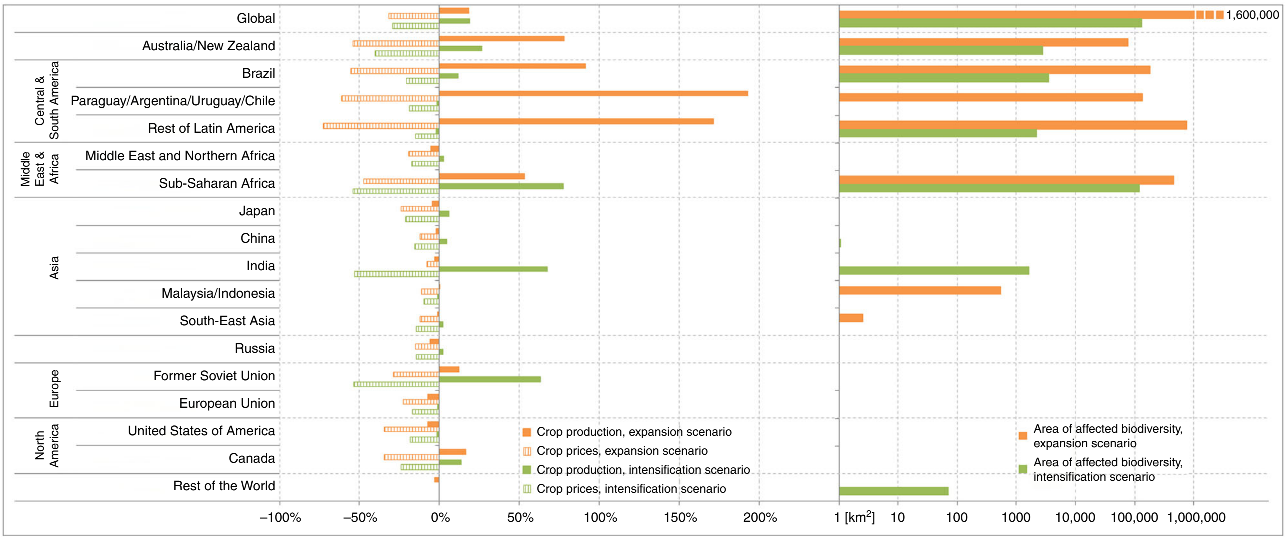

Fig. 2 Impacts of expansion and intensification on production, prices and area of affected biodiversity. The left panel shows the change in crop production and prices under expansion and intensification scenarios compared to the reference scenario in 2030, accounting for current trends in population growth, gross domestic product and trade policies. The right panel shows the area of land where the top 10% of the most biodiverse regions are threatened under the expansion and intensification scenario (*x*-axis for area is scaled logarithmically)

Nepal, Myanmar and China where farming intensity was projected to increase substantially until 2030 (Fig. 3b). While hotspot patterns for birds and mammals showed high spatial agreement (64 and 66% overlap for cropland expansion and intensification, respectively), the areas of high agricultural potentials associated with high endemism richness were relatively smaller for amphibians (41 and 40% overlap with the other taxa) due to their smaller ranges concentrated in specific geographical areas.

Agricultural intensification affects species not only in croplands but also in surrounding habitats, thus the impact will likely differ for species with different habitat requirements (e.g. forest specialists are unlikely to reside in significant numbers within existing farmland). Consequently, we used information on species preferred habitat types and examined spatial associations between intensification and biodiversity for (1) species that are regular or at least marginal cropland users vs. (2) forest or natural habitat specialists (Fig. 4). As expected, the intensification pressure was more pronounced for cropland users (significant hotspots covering 8% of the terrestrial ecosystems; Fig. 4a) than for forest or natural habitat specialists (4%, Fig. 4b), especially in the Chaco ecoregion of South America, Central and Eastern Africa and Southern Asia. However, the general hotspot patterns remained largely consistent, suggesting that areas with high endemism richness in general hold high diversity of forest or natural habitat specialists as well as high diversity of cropland users.

The associations of low agricultural potentials and low endemism richness (i.e. cold spots) showed consistent patterns for both scenarios across all three taxonomic groups (Fig. 3). The cold spots were identified mostly on non-arable, desert, or ice-covered land, but also in industrialised agriculture in North America and Western Europe, where further increases of yields are limited (53 and 48% of land surface for expansion and intensification, respectively). Other regions with high agricultural potentials were either not significant or occurred in areas with comparatively low biodiversity (high–low associations), e.g. the Midwest of North America, Former Soviet Union, Sub-Saharan Africa (Fig. 3a; 9% of terrestrial ecosystems) and, for the intensification scenario, also large parts of India and China (Fig. 3b; 15% of terrestrial ecosystems), where our simulations show high production gains in the intensification scenario (Fig. 2). However, these high intensification regions with relatively low global biodiversity were much smaller when focusing on cropland species (5% of land surface) as opposed to forest or natural habitat specialists (11% of land surface), being restricted mostly to Former Soviet Union and China (Fig. 4a).

We then examined the same top 10% areas for cropland expansion and intensification as in the economic analysis and overlaid them with the biodiversity data above the 10th percentile to identify regions where the highest endemism richness coincides with the highest potential pressure from land expansion and intensification.

These ‘hottest hotspots’ where the highest biodiversity may be particularly threatened by future cropland expansion and intensification, were found especially in Central and South America (affecting an area of 1.097 million km^2), Sub-Saharan Africa (773,375 km^2) and Australia (79,490 km^2). Cropland expansion affected biodiversity hotspots mainly along the tropical Andes, the Brazilian Atlantic forest and in West and East Africa (Fig. 5). For the intensification scenario, the areas with the highest risk of biodiversity loss were located in Sub-Saharan Africa (122,702 km^2) and Brazil (3,560 km^2). In total, cropland expansion was likely to affect much larger areas (1.6 million km^2) with the highest conservation value than cropland intensification (132,984 km^2) (Figs. 2 and 5b, Supplementary Table 5). For intensification, these potential conflict areas, however, would be 2.4 times larger for cropland species than for forest and natural habitat specialists (Supplementary Fig. 19). On the other hand, large areas with high cropland expansion potential exist in Paraguay, Argentina, Uruguay and Chile (1.176 million km^2), Sub-Saharan Africa (894,178 km^2) and Brazil (871,759 km^2), that do not overlap with the top 10% values of biodiversity (Supplementary Table 5). Sub-Saharan Africa also holds most of the top 10% areas for intensification (673,300 km^2) that do not at the same time belong to the top 10% of biodiverse areas.

Changing the (arbitrary) percentile threshold from 5 to 30% led to a considerable increase in the conflict area (especially in Latin America for expansion and in East Africa and South Asia for intensification; Supplementary Fig. 18), with a substantially steeper slope for expansion than for intensification (Fig. 5b).

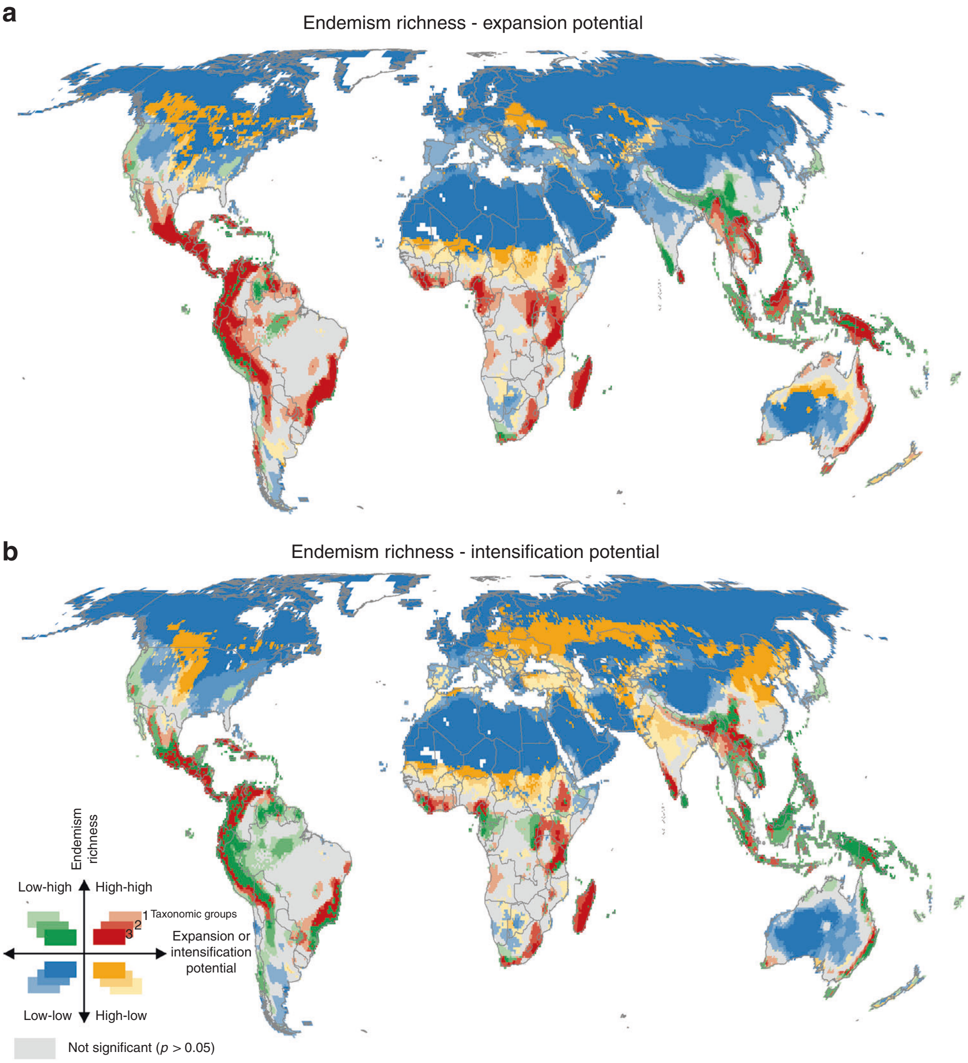

Fig. 3 Spatial association between endemism richness and potentials for **a** cropland expansion and **b** intensification. They are calculated using local indicators of spatial association (LISA) at 55-km resolution. High–high clusters indicate hotspot locations (red), in which areas most suitable for 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 colours indicate significant results for one, two or all three taxonomic groups (birds, mammals, amphibians)

Discussion

Here, we applied an iterative coupling approach[6], accounting for both cropland expansion and intensification specifically designed to be equivalent in terms of reaching the same production targets. For consistency, we assumed neither costs of expanding cropland nor costs for intensifying production. We quantified the impact of both strategies on agricultural markets by taking trade as well as feedbacks between supply and demand into account and identified areas most susceptible to biodiversity loss, using an integrated approach that combined global economic analysis with fine-scale agro-ecological model simulations (30 arc-sec resolution) and a broader-scale biodiversity measure (55-km resolution).

Our analyses showed substantial trade-offs between cropland expansion and cropland intensification scenarios and their impacts on crop production and biodiversity. From an economic point of view, both scenarios contributed to improved food security in terms of increased production and lower prices not only in places where crop production rose (e.g. Sub-Saharan Africa or Australia under both scenarios) but also in regions that increased import of crops due to lower world market prices. However, contradicting impacts were apparent in several regions, most notably in Latin America with rising production under the cropland expansion scenario and decreasing production under the intensification scenario, or in India and China with the opposite effects. In addition, we saw contrasting impacts on trade flows under the two scenarios: The European Union and India turned from a net-importer in the cropland expansion scenario to a net-exporter in the intensification scenario. With respect to food consumption, regions affected by food insecurities (e.g. South-East Asia and Sub-Saharan Africa) changed consumption to a different degree under the two scenarios. Food consumption in India and to a smaller degree in Sub-Saharan Africa increased more under the intensification scenario (+35 and 28%, respectively) compared to the expansion scenario (+4 and 21%, respectively), while in the rest of South-East Asia both scenarios resulted in an increase of about 7% (Supplementary Fig. 16). For South and Central American countries, the cropland expansion scenario is clearly the beneficial strategy with respect to food security.

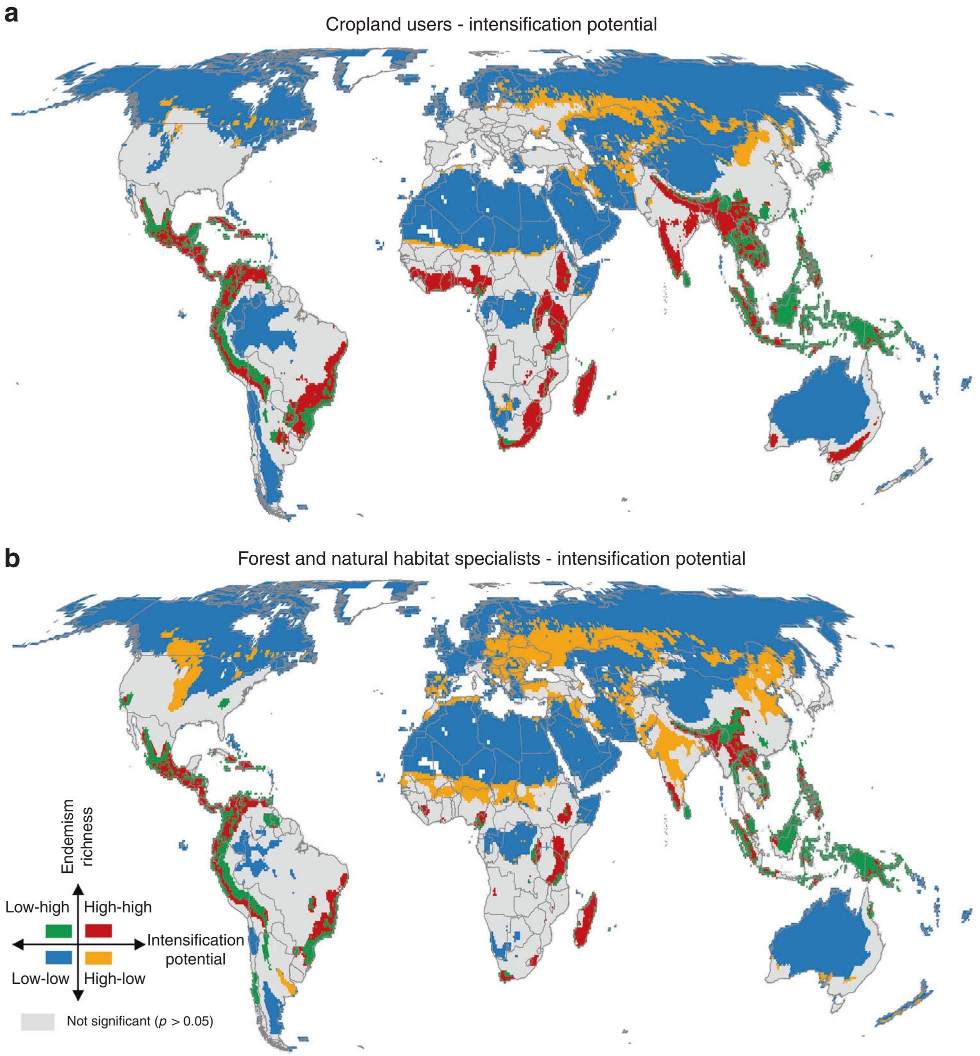

Fig. 4 Spatial association between potentials for cropland intensification and endemism richness for **a** regular or marginal cropland users and **b** forest or natural habitat specialists. They are calculated using local indicators of spatial association (LISA) at 55-km resolution. High–high clusters indicate hotspot locations (red), in which areas most suitable for intensification of cropland are significantly associated with high values of cropland users/forest or natural habitat specialists (at 0.05 significance level). Low–low clusters (blue) show cold spot locations, in which areas with low potential for intensification are associated with low values of cropland users/forest or natural habitat specialists. High–low and low–high clusters show inverse spatial association

From a biodiversity point of view, the projected cropland expansion and intensification will likely occur in many regions that are valuable for biodiversity conservation. These pressure hotspots were found mostly in tropical ecosystems of Latin America, Central Africa and South-East Asia that were previously identified as areas where biodiversity is most threatened by agricultural production[29,31,35,47]. However, our calculations highlighted different hotspots of potential future conflict for the two agricultural pathways. Cropland expansion threatened biodiversity most in Latin America and Central Africa that contain large, relatively intact natural habitats with biophysical and socio–economic conditions likely to promote cropland expansion in the next decades. On the other hand, cropland intensification is likely to affect considerably smaller areas with the highest endemism richness in comparison to cropland expansion (~20-fold difference for the 10% threshold). But these top-pressure places include often overlooked regions in India, Myanmar or East Africa where existing small-scale cropping systems have high potential for further intensification but in the same time harbour substantial biodiversity, typically under no form of formal protection.

Indeed, we found relatively little coverage of our agriculture–biodiversity hotspots by terrestrial protected areas listed in the World Database on Protected Areas (WDPA, IUCN categories I-VI). The overlap of the hottest hotspots with the WDPA[48] showed that <35% (625,000 km^2) of these hotspots are currently protected. While almost half of these areas are under strict protection (agriculture restricted; IUCN class Ia, Ib, II), the other half is less strictly protected (agriculture partly allowed; IUCN classes III, IV, V, VI). However, more than 65% of the hottest hotspots are currently not protected (especially in the tropical regions of Africa), accounting globally for 1.2 million km^2 of land. Our analysis showed that these areas consist mainly of hotspots for cropland expansion, while 92% of the conflict hotspots for intensification are already under protection (Supplementary Note 6). As previous research found that even more proactive conservation schemes (e.g. Last of the Wild) may overlook many at-risk regions[47], this suggests the need for incorporating future agricultural projections into current conservation prioritisation schemes, in order to protect highly biodiverse but agriculturally desirable areas. We also tested the effect of a policy scenario that would restrict cropland expansion to

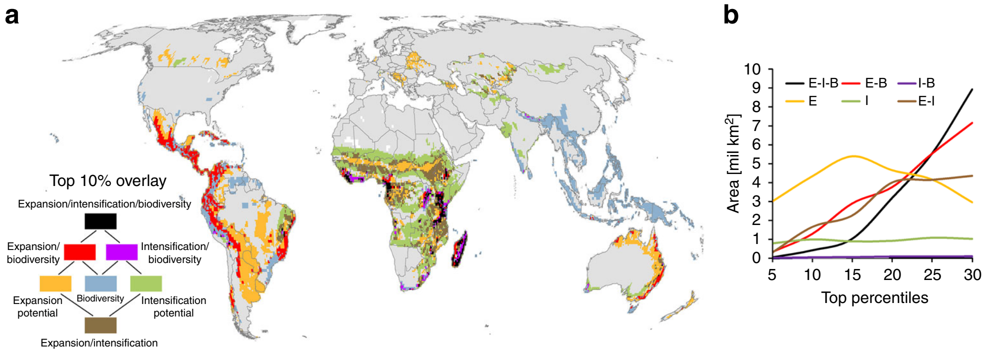

Fig. 5 Quantile overlay of expansion potential, intensification potential and endemism richness. While **a** shows the 10th percentile, **b** shows the sensitivity of the overlay based on selected thresholds between 5 and 30% (see Supplementary Fig. 18 for maps of the different thresholds). The overlay analysis was performed at 55 km resolution of an equal-area grid. The red areas highlight the hottest hotspots, where high biodiversity may be particularly threatened by future cropland expansion. The purple areas highlight the hottest hotspots, where high biodiversity may be particularly affected by future cropland intensification. The black areas pinpoint places where high biodiversity is particularly threatened by both agricultural scenarios simultaneously. The orange, green and blue colours indicate regions with the top 10% of expansion potential, intensification potential and biodiversity that do not overlap with any other top 10% of data. The brown areas indicate regions where the top percentile of expansion and intensification potential overlap without overlapping the top percentile areas of biodiversity. In **b**, the same colours are used, abbreviating expansion (**E**), intensification (**I**) and biodiversity (**B**)

unprotected areas. While the relative changes of expansion area between the two expansion scenarios are relatively small at global scale, the changes range between +10% and −3% for regions with expansion areas greater 100,000 km^2. Strongest absolute reductions in the policy scenario which restricts cropland expansion occurred in Sub-Saharan Africa (70,000 km^2), Rest of Latin America, and Australia/New Zealand (13,700 km^2 each). Additional expansion took place in Brazil (76,600 km^2) and Canada (10,500 km^2) (Supplementary Note 7).

In combination, our results from the economic and biodiversity analyses demonstrated that while cropland expansion will in most cases affect areas important for conservation (regions with the highest production gains in Central and South America (Fig. 2) have significantly high endemism richness (Figs. 3a, 5a), cropland intensification is possible in areas with lower biodiversity (regions with the highest production gains in Sub-Saharan Africa, Central India, Northeast China and Former Soviet Union (Fig. 2) occur in globally less biodiverse regions (Figs. 3b, 5a). These regions largely coincide with the extensive cropping land system archetype[24], where large production gains could be achieved by closing yield gaps through nutrient and water management[36] without necessarily promoting additional decline in biodiversity on the current or future farmlands, e.g. via the use of precision or climate smart agriculture. However, previous studies cautioned against such generalised conclusions about sustainable intensification[35,49,50]. Sub-Saharan Africa and Former Soviet Union are heterogeneous regions that still harbour valuable diversity of species. Even though they are not recognised as biodiversity hotspots globally, largely due to the latitudinal gradient of species richness, many places in Eastern Europe are considered strongholds of agricultural biodiversity on the continent, especially when compared to industrialised farmland in other parts of Europe[51,52]. Therefore, it is likely that the regionally important biodiversity, especially of farmland species, would face the risk of extinction if the extensive forms of farming were replaced by intensive agriculture. This risk would be even exacerbated if agricultural intensification reduced crop genetic diversity, e.g. by encouraging farmers to switch from diverse landraces to hybrids. This, in turn, may reduce field-scale diversity of many taxa in agroecosystems due to a narrower range of food resources and homogenization of crop architecture[53,54]. Again, this shows the need for proactive consideration of different possible farming systems in terms of both expansion or intensification and more detailed and context-specific analyses that consider also other ecosystem services, such as carbon sinks, and resilience of the land-use systems to conclude whether and how regions could be used for expansion or could be intensified sustainably[55].

Integrated approaches that estimate global land-use change, such as the approach used here, are inherently associated with multiple sources of uncertainties and largely depend on the quality of input data[56–58]. First, although we used the best available determinants of cropland expansion and intensification potentials, uncertainties in global data on land-use and land-use intensity (such as crop yields, harvested area, etc.) at a fine spatial scale remain a major challenge[59,60]. Second, infrastructural, societal, cultural or political aspects that determine accessibility of land (e.g. due to transportation costs, land tenure, traditional or indigenous land or land in failed states) may determine the realisation of estimated agricultural potentials but are not considered due to a lack of global data. Also, all estimated changes especially for cropland intensification assumed that countries have the economic, technological, infrastructural and institutional means to intensify agricultural production, which could be questioned especially in regions like Africa, where we identify large areas with the highest potential for cropland intensification. Third, our models provide cropland expansion and intensification potentials at a 30 arc-second resolution, but the best currently available global measures of biodiversity distribution are not available at such fine scales. The 55-km grid cells are already on the verge of acceptable accuracy because aggregations of species ranges at scales below 2 arc-degrees of resolution may overestimate species richness[61]. Here we alleviated this issue by staying away from a simple measure of species richness and put emphasis on endemism (i.e. range sizes of species within an assemblage), knowing that hotspots of species richness are typically not congruent with endemism or threat[62]. This approach also avoided the utilitarian assumption that landscapes with the most species have the highest conservation value[63]. However, we cannot be certain that the habitats at risk from cropland expansion or intensification in each 55-km grid cell are the same ones in which species occur. For example, hotspot regions in the tropics may have valuable habitats distributed along an elevation gradient but only lowland habitat may be under pressure because topographic, soil and accessibility conditions restrict agricultural suitability in highlands. Nonetheless, our approach allows for exchanging or adding biodiversity data from other sources, e.g. when more recent or higher-resolution data are available. Fourth, in contrast to biodiversity models, such as GLOBIO that use empirically derived matrix of changes in mean species abundances following a land transformation[64], our approach highlights the main areas at risk, ignoring the mechanisms how expansion or intensification threatens biodiversity. The impacts of continuing land conversion are often non-linear and can vary with spatial configuration[19,65], while indirect effects of intensification threaten biodiversity beyond agricultural lands, due to agrochemical run-offs, habitat homogenization or introduction of invasive species[11,14]. Various aspects of these uncertainties in our integrated approach could be addressed, for example, by applying our method to past data and comparing the identified hotspots with e.g. cropland expansion data derived from remote sensing.

Despite these caveats, our study provides a global perspective of the complex trade-offs between cropland expansion, intensification and biodiversity. Contrasting two scenarios of future production growth clearly demonstrates that each scenario leads to fundamentally different levels and spatial patterns of crop production and prices as well as distributions of the most at-risk areas. Arguably, it is unrealistic to assume that identified hotspot regions will curtail cropland expansion or intensification when there are pressing needs for food or income[65]. However, it can be realistically assumed that best management practices implemented locally or sustainable goals coordinated internationally will help harmonising biodiversity conservation and agricultural production[19].

Our results also provide global-scale spatially explicit contribution to the still unresolved debate on land sharing vs. land sparing[66–68]. Similar to the social-ecological systems model approach[69], we move forward from the bipolar framework by treating agricultural landscapes as complex social-ecological systems, accounting for socio–economic aspects of food production, and stressing the conservation value of biodiversity. Assuming a global land sparing approach, regions where high agricultural potentials were associated with low levels of endemism richness (orange High–Low clusters in Fig. 3) may be suitable for increased crop production at relatively small trade-offs with biodiversity compared to other regions, which could open up the scope for sparing in regions with biodiversity hotspots that would be otherwise threatened by agricultural pressure in the near future.

Even though land-use decisions are made at much finer scales, we identified global hotspots where the debate is most relevant and where additional studies should investigate on a more regional to local level[70]. Because global-scale results are rarely directly transferable to finer spatial scales[71], this should be done by employing regional biodiversity data and downscaled economic analyses, although with the drawback that regional CGE models are limited in considering bilateral trade flows. Moreover, policy decisions aiming at harmonizing agricultural production and conservation, such as land conversion zoning or financial incentives, will have to consider also non-provisioning ecosystem services, rural development objectives, and regional cultural conditions, as well as social and economic implications of, e.g. different strategies for intensification[72]. At the same time, stable governance and effective international organisations are needed to support the implementation of sustainable agricultural strategies because smart land management is a key lever to achieve multiple Sustainable Development Goals[20]. However, identifying the hotspots where future conflicts between biodiversity and agriculture are likely to arise is a first essential step to aid sustainability policies and conservation prioritization schemes. This is also becoming increasingly important with regard to efforts for increasing future bioenergy demand[73] and negative emission scenarios, by use of bio-energy carbon capture and storage (BECCS) technologies[74]. Integrative approaches, such as the one presented here, support the calls for assessing the trade-offs in alternative agricultural pathways and can ultimately help us to meet production goals while maintaining our vital life-support systems.

Methods

We iteratively link a global CGE model and a dynamic crop growth model to determine the impacts of cropland expansion and intensification on agricultural markets. Cropland expansion and intensification potentials for 2030 are used to identify spatial associations with areas of high biodiversity value (Fig. 1).

Integrated agricultural potentials. Our integrated approach combined biophysical and socio–economic conditions to create maps of future agricultural expansion and intensification potentials at 30 arc-sec resolution. The biophysical data covered the period 2011–2040 and considered climate change; the time horizon of the socio–economic data was 2007–2030. The biophysical expansion potential[29] was determined by combining a crop suitability approach for 17 economically important staple and energy crops[37] (Supplementary Table 1) with land availability for cropland expansion, which included all suitable land that is not yet under cultivation[1] or urbanised[75]. We integrated FAO forecasts on expansion[76], that also consider regional socio–economic condition, by using them to weight the biophysical expansion potentials. For details, see Supplementary Note 2.

In case of intensification, biophysical potential yields for the 17 crops were globally simulated on today's cropland[1] using the crop growth model PROMET[6,77]. The ratio between biophysical potential yields and statistical yields[22] resulted in a biophysical intensification potential. These were combined with the marginal profitability of crops that depend on socio–economic scenarios (Supplementary Note 1) that were implemented into the computable general equilibrium model DART-BIO to allocate crops by maximising profit[6]. This resulted in integrated intensification potentials that were used to feed back to the DART-BIO model in terms of changed agricultural productivities, which in turn altered the marginal profitability of crops, such that the re-allocation was repeated iteratively until a stable allocation was established. The integrated model coupling approach allowed to account for changes in land allocation of crops over time due to changing cropping decisions of farmers that depend on changing demand (e.g. population growth, food consumption behaviour) and supply (e.g. climate change, technological progress). For details, see Supplementary Note 3.

Impact on agricultural markets. We extracted the top 10% of areas with the highest integrated expansion and intensification potentials to create comparable scenarios of future agricultural pathways. The expansion scenario allowed 7.3 million km^2 of land to be converted into farmland in places with the highest 10% of expansion potential. The intensification scenario allowed closing yield gaps on 10% of land with the highest intensification potential, up to a level that resulted in the same global production gain. We applied both scenarios in the CGE model DART-BIO to quantify their impact on agricultural markets in terms of crop production, prices, trade and consumption. CGE models solve for balance between supply and demand with flexible prices. For reference, we compared the impact to a 2030 reference scenario that carried forward current trends in demographic growth, gross domestic products and trade policies taking into account that with higher incomes preferences change towards e.g. livestock products. For details, see Supplementary Note 4.

Agriculture–biodiversity hotspots. For biodiversity data, we used global range maps for 19,978 species of birds, mammals and amphibians derived from the International Union for Conservation of Nature[78] and Birdlife databases[79]. From these maps, we calculated endemism richness (sum of the inverse extents of occurrence of all species present in a grid cell) because, unlike other biodiversity measures, endemism richness indicates the relative importance of a landscape for conservation by combining aspects of species richness and geographic range size[80]. The data were aggregated in an equal-area grid of 55 × 55 km to provide sufficient detail for global analysis but limit excessive false-presence errors that occur at aggregations of range maps at resolutions below 2 arc-degrees[61]. The hotspots where global biodiversity could be most affected by near-future farmland expansion and intensification were analysed using Local Indicator of Spatial Association (LISA) and quantile overlay. For details, see Supplementary Note 5.

Reporting summary. Further information on research design is available in the Nature Research Reporting Summary linked to this article.

Data availability

Raw datasets analysed in this study are publicly available from the sources provided in Supplementary Note 8 in the supplementary information. All relevant data generated during the study are available upon request from the authors.

Code availability

The code of the DART-BIO model and for coupling DART-BIO and PROMET is available upon request. PROMET code is not publically available.

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Author contributions

T.V., R.D., F.Z. and R.S. conceived the study and designed the research. R.D., F.Z., T.V. and J.S. collected and analysed the data. R.D. conducted the DART-BIO simulations. T. V. conducted the LISA and biodiversity overlay analysis. F.Z., J.S., W.M. conducted the PROMET simulations and the suitability analysis. R.D. and F.Z. conducted the model coupling between DART-BIO and PROMET. T.V., R.D., F.Z., J.S. and R.S. prepared the manuscript. All authors discussed the results and commented on the paper.

Additional information

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