



Global patterns of agricultural land-use intensity and vertebrate diversity

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ABSTRACT

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

Location Global.

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

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

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

Keywords

Biodiversity conservation, endemism richness, global agriculture, land-use change, land-use intensity, sustainable intensification.

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INTRODUCTION

For more than 10,000 years, land use has played a crucial role in the development of human societies. Humans rely on agriculture and forestry for food, fibre and bioenergy (Ma, 2005) and have already modified 75% of the Earth's ice-free terrestrial surface of which 12% is dedicated to cropland and 22% to pasture (Ramankutty *et al.*, 2008), with less than a

quarter remaining as wildlands (Ellis & Ramankutty, 2008). This is expected to escalate further, as demand for biomass will increase drastically in the coming decades due to growing human population, surging consumption, changing diets and demand for bioenergy (Ellis & Ramankutty, 2008; Pereira *et al.*, 2010; Smith & Zeder, 2013). Even under ambitious future scenarios of reducing food waste, consumption of meat and dairy, and inequality, production increases and

related land-use change will still be necessary (Visconti *et al.*, 2015). This is problematic because land-use change is the main driver of the ongoing biodiversity crisis, primarily via habitat loss and fragmentation (Sala *et al.*, 2000; Foley *et al.*, 2005) but also via the introduction of exotic species (Clavero & García-Berthou, 2005; Ellis *et al.*, 2012) and increased hunting due to access from new road construction (Laurance *et al.*, 2009). In general, biodiversity loss can have repercussions on ecosystem functioning (Tilman *et al.*, 2012), resilience of socio-ecological systems (Ma, 2005) and the welfare of human societies (Ma, 2005; TEEB, 2009). Therefore, understanding land-use effects on biodiversity is of prime importance.

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

For the purpose of our study, we define agricultural land-use intensity as the degree of adoption of land management practices enabling yield increases from a given area of agricultural land (Matson *et al.*, 1997; Ellis *et al.*, 2013). Yields are a commonly used measure of land-use intensity (hereafter: LUI). Yet, different practices can result in yield increases. For example, increasing fertilizer, mechanization or irrigation may have different environmental outcomes. Moreover, regions with similar yields should not be considered equally intensive if these regions differ in bioclimatic conditions which can constrain agriculture (e.g. potential yields, Neumann *et al.*, 2010). As such, LUI is a multidimensional issue that relates to a range of individual processes linking people and the land and therefore cannot be fully represented by only one metric (Erb *et al.*, 2013 and Kuemmerle *et al.*, 2013 for full reviews).

Different intensification processes can vary substantially across the globe, as do their effects on biodiversity (Foley *et al.*, 2005; Chapin *et al.*, 2008). Intensive agriculture can have particularly detrimental effects on biodiversity (Benton *et al.*, 2003; Alkemade *et al.*, 2010), including negative effects on species richness (Herzon *et al.*, 2008; Flynn *et al.*, 2009), population size (Donald *et al.*, 2001) and the loss of functional diversity (Herzon *et al.*, 2008; Flynn *et al.*, 2009). Fertilizers have been shown to negatively affect biodiversity and, along with pesticides, pose a substantial threat to biodiversity for birds, mammals and amphibians (Kerr & Cihlar, 2004; Gibbs *et al.*, 2009; Kleijn *et al.*, 2009; Hof *et al.*, 2011). Irrigation causes salinization of soils which can prove toxic to plants with cascading effects on ecosystems (Yamaguchi & Blumwald, 2005), while intensive livestock grazing can have detrimental effects on biodiversity (Alkemade *et al.*, 2012) especially when

pastures lack remaining native vegetation (Felton *et al.*, 2010). In contrast, small-scale agro-ecological production practices, which often use less agro-chemical inputs, have been found to be less destructive to biodiversity than industrial practices on a per area basis (Perfecto & Vandermeer, 2010).

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

Such knowledge gaps are alarming as a large proportion of global land-use change has historically occurred along intensification gradients (Rudel *et al.*, 2009). Particularly since the 1950s, intensification has accelerated rapidly, with irrigated lands increasing twofold (FAOSTAT, 2010) and fertilizer application up to fivefold (Tilman *et al.*, 2001). As fertile land becomes scarce and environmental costs of converting natural habitat into agricultural land less acceptable, further intensification of existing agricultural land is likely. Indeed, 'sustainable intensification' pathways are gaining considerable support (Foley *et al.*, 2011; Mueller *et al.*, 2012). As production is higher on intensified agricultural land, this could, in theory, result in less overall pressure on natural ecosystems, that is a land sparing effect, leading to more land potentially set aside for conservation (Green *et al.*, 2005). However, a land sparing effect is not guaranteed and is only possible in combination with strong governance (Byerlee *et al.*, 2014).

Recent developments in framing LUI (Erb *et al.*, 2013; Kuemmerle *et al.*, 2013), high-resolution LUI datasets (see Appendix Panel S1 in Supporting Information) and global biodiversity metrics (Kier *et al.*, 2009) all provide new opportunities for analysing how spatial patterns in LUI relate to biodiversity patterns. Here, we acknowledge the multifaceted nature of LUI and compare global patterns of biodiversity with a suite of thirteen agricultural LUI metrics (Panel S1 and Table S1), each of which represent different dimensions of LUI. As our biodiversity metric, we chose endemism richness (Kier & Barthlott, 2001) for birds, mammals and amphibians, which is an indicator of the importance of a grid cell for conservation and combines aspects of species richness and geographic range size.

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

METHODS

Global land-use intensity datasets

We compared thirteen land-use datasets measuring different aspects of agricultural intensity. Our datasets are from circa

the year 2000 – the time period where such datasets are richest at the global scale (Table S1, Kuemmerle *et al.*, 2013). To group our intensity metrics, we utilized the classification scheme of Kuemmerle *et al.* (2013) where LUI metrics are split into three categories related to inputs, outputs and system metrics. Input metrics refer to the intensity of land use along different input dimensions, such as fertilizer and irrigation. Output metrics relate to the ratio of outputs from agricultural production and inputs, for example yields (harvests/land). System-level metrics describe the relationship between the inputs or outputs of land-based production to the overall system, for example yield gaps (actual vs. attainable yield).

For input metrics, we chose a cropland extent map (Panel S1, Ramankutty *et al.*, 2008), which combines national and subnational agricultural inventory data with satellite-derived land cover data and forms the basis for yields and harvested areas of 175 of the world's major crops (see Monfreda *et al.*, 2008). For irrigated cropland, we used a dataset which accounts for areas equipped for irrigation (Panel S1, Siebert *et al.*, 2005). We also used the most fine-scale nitrogen fertilizer input dataset available (kg N/ha applied to croplands, Panel S1, Potter *et al.*, 2010).

For output metrics, we selected crop yields for maize, wheat and rice (Panel S1, Monfreda *et al.*, 2008), because together, they represent approximately 85% of global cereal production (Hafner, 2003). Palm oil- and soya bean-harvested areas (Panel S1, Monfreda *et al.*, 2008) were also included due to their expansion in the tropics and considerable conservation concern (Gasparri *et al.*, 2013; Wilcove *et al.*, 2013). We included livestock heads per km² using the 'Gridded Livestock of the World' database (Panel S1, Wint & Robinson, 2007).

For system-level metrics, we included yield gaps for maize, wheat and rice (Panel S1, Neumann *et al.*, 2010) and human appropriation of net primary productivity (HANPP, Panel S1, Haberl *et al.*, 2007). System metrics differ from output metrics in that they relate inputs or outputs to system properties. While system metrics thus capture the intensity of the land system as a whole, they do so at the cost of obscuring individual properties of intensification. Yield gaps here refer to the difference between the actual yield (Panel S1, Monfreda *et al.*, 2008) and estimated potential yield (t/ha) calculated by integrating biophysical and land management-related factors (Panel S1, Neumann *et al.*, 2010). To interpret yield gaps in the same way as our other intensity metrics, we took the inverse of yield gaps so that higher numbers (i.e. lower yield gaps) relate to higher LUI. We additionally chose HANPP, as it provides a measure of the percentage of NPP that humans extract from the land, thus providing an indicator of the impact of agricultural management on ecosystems in terms of the inputs and outputs of land-based production (Panel S1, Haberl *et al.*, 2007).

Global biodiversity datasets

Endemism richness for bird, mammal and amphibian diversity was created from expert-based range maps (Panel S1,

Birdlife, 2012; IUCN, 2012). We scaled the data to an equal area grid of 110 × 110 km (approximately 1 degree at the equator) as finer resolutions are not recommended at the global scale due to an overestimation of species occurrences (Hurlbert & Jetz, 2007). We chose endemism richness (Kier & Barthlott, 2001; Kier *et al.*, 2009) as it combines aspects of both species richness and species' range sizes within an assemblage. Endemism richness was calculated as the sum of the inverse global range sizes of all species present in a grid cell.

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

Analysing the spatial patterns of land-use intensity and biodiversity

All LUI datasets were rescaled to the 110 × 110 km resolution of the endemism richness datasets by taking the mean value for each grid cell. We overlaid the different LUI maps with endemism richness. This allowed us to explore differences in emerging patterns, depending on LUI metrics and taxonomic classes for mammals, birds and amphibians. We then delineated high-pressure regions of high LUI and high endemism richness by abridging datasets to the top 2.5% of the distribution, following the hotspot definition of Ceballos & Ehrlich (2006). We used the LUI datasets to generate maps of high-pressure regions by intersecting all LUI metrics with endemism richness. To differentiate the importance of individual LUI metrics in high-pressure regions, we created flower charts by calculating the relative values (in percentiles) per LUI metric (Figs S1 and S2 show the top 2.5%, 5% and 10% hotspot maps for each metric, and top 2.5% hotspot information is shown in Table S2).

To complement the qualitative approach with statistical quantifications, we calculated the spatial associations between LUI and endemism richness using the bivariate Moran's I metric, also known as a local indicator of spatial association (LISA; Anselin, 1995). This metric indicates the spatially explicit strength of associations between two variables and results in (1) high-high values, here, where high endemism richness is surrounded by neighbouring cells of high LUI, (2) high-low values, high endemism richness surrounded by low LUI, (3) low-high and (4) low-low (results for all metrics are provided in Fig. S3). The strength of the relationship was measured at the 0.05 level of statistical significance calculated by a Monte Carlo randomization procedure based on 999 permutations (Using GeoDa 1.4 software). Associating endemism richness values with intensity metrics in the neighbouring cells is important because simple cell overlap (used to create the concordance maps) can be affected by differences in spatial resolution or noise in the data. We used the

resulting statistically significant areas to generate summary maps of high- and low-pressure regions for all metrics (Figs 2 and S4).

RESULTS

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

In relation to our second research question, regions of potential conflict between different aspects of high LUI associated with high endemism richness were found primarily in

the tropics, with different combinations of high LUI metrics associated with high endemism richness. For example, for input metrics associated with high endemism richness, high fertilizer use was found in China, Southeast Asia and Europe, and irrigation was concentrated in large areas of the United States, India, the Middle East and China (Fig. 1).

Regarding output metrics, high livestock densities were found in large regions of Latin America and India (Fig. 1). Palm oil plantations showed high concordance with endemism richness patterns, exerting substantial pressure in most areas where palm oil is grown, especially in Nigeria, the Republic of Guinea, Malaysia and Indonesia (Fig. 1). Pressure on endemism richness from high-intensity soya bean cultivation was particularly high in Brazil, Argentina and Indonesia (Fig. 1). Rice yields had the highest area of overlap

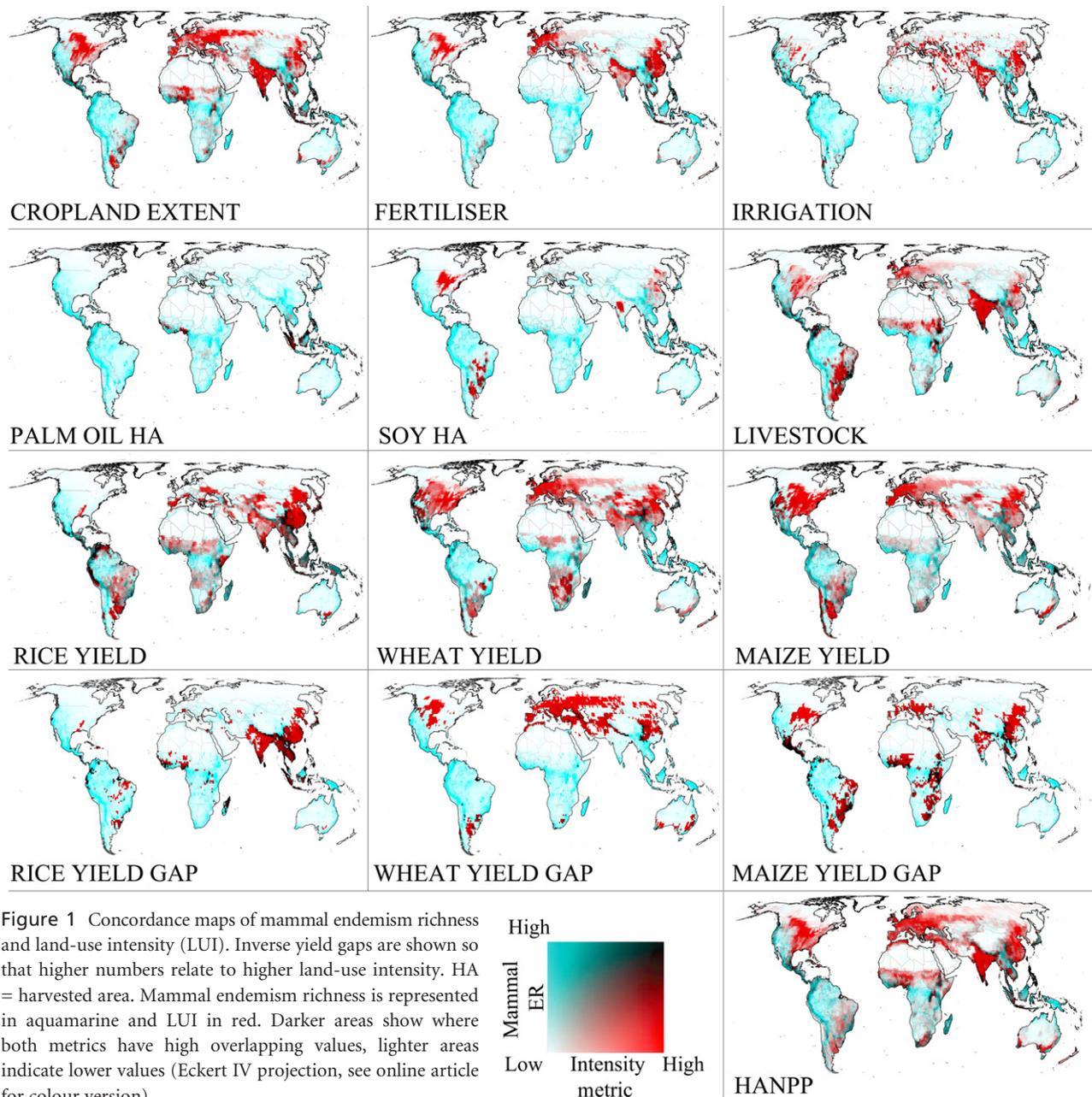


Figure 1 Concordance maps of mammal endemism richness and land-use intensity (LUI). Inverse yield gaps are shown so that higher numbers relate to higher land-use intensity. HA = harvested area. Mammal endemism richness is represented in aquamarine and LUI in red. Darker areas show where both metrics have high overlapping values, lighter areas indicate lower values (Eckert IV projection, see online article for colour version).

with endemism richness (Fig. 1). Over 50% of total land cover in the Indomalayan region and 20% of the Neotropics were found to have both high rice yields and high endemism richness (Fig. S5, from statistically significant local indicators of spatial association).

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

High endemism richness associated with low LUI were found in many tropical regions (Figs 1 and S3). Specifically, high yield gaps due to currently low levels of irrigation and fertilizer input (Mueller *et al.*, 2012) were found in Southeast Asia, Mesoamerica and sub-Saharan Africa. Concordance of low HANPP and high endemism richness occurred in large regions of the tropical Andes, the Amazon, Central Africa and Southeast Asia (Figs 1 and S3). Conversely, our analyses showed that developed countries with an industrialized agricultural sector such as Europe and North America had particularly high LUI coupled with comparatively low endemism richness (Figs 1 and S3).

When comparing between mammals, birds and amphibians, broad patterns of endemism richness were remarkably similar and highly correlated. All biodiversity metrics were found to have positive and significant Spearman's rank correlation coefficients ($P < 0.05$) of over 0.84, including between endemism and species richness (Table S3). Mammals and birds showed exceptionally high correlations, both for endemism richness (0.95) and species richness (0.96). In terms of spatial patterns of high endemism richness congruent with LUI, relatively small differences were found between taxonomic classes. Most differences were found for amphibians, where small species ranges resulted in smaller areas associated with high LUI compared to birds and mammals (Fig. S6). Amphibians were the only taxon found that coincided with high yields and high HANPP in the South-eastern USA. In the Caucasus, mammals were the only taxon present in concordance with high LUI (for all metrics, see Fig. S3). Birds stood out as not having any areas of high endemism richness associated with high LUI in Europe, where mammals and amphibians coincided with high LUI in areas of the Alps, the Pyrenees and parts of Italy. Birds also exhibited higher concordance with livestock in Latin America and cropland extent in South-eastern Australia than other taxonomic classes. Overall, birds and mammals showed strikingly similar spatial patterns, where ~80% of high mammal endemism richness associated with high LUI overlapped with high bird endemism richness.

When comparing between LUI metrics, the highest correlation was found between cropland extent and fertilizer use (0.92, Table S3). With the exception of wheat yield gaps and palm oil-harvested area, all LUI metrics had positive correlation coefficients. However, over half of the correlations between LUI metrics were below 0.5. Correlations between

taxonomic classes were higher than those found between most LUI metrics. Correlations between biodiversity indicators and LUI metrics were highest for livestock density, HANPP and maize yields.

To identify regions where any one LUI metric was associated with one or more taxonomic classes, we combined individual results of local indicators of spatial association (LISA) by LUI metric and taxonomic class (see Fig. 2 for combined taxa and Fig. S7 for mammals, birds and amphibians separately). When these results were compared with CI hotspots, we found that over half (~55%) of CI hotspots (Mittermeier *et al.*, 2004) fell within our regions of high LUI and high endemism richness. However, substantial areas of high endemism richness, for all three taxonomic classes, and high LUI were highlighted which are not currently contained within CI hotspots and include Papua New Guinea (due to high maize and rice yields), Venezuela (high maize and rice yields and livestock density), parts of China (fertilizer, irrigation, livestock density and wheat, maize and rice yields), Eastern Africa (wheat yields and livestock density) and Eastern Australia (maize yields, HANPP and livestock density).

We then investigated areas of potential conflict between high LUI and high endemism richness by overlaying the top 2.5% of our metrics' geographic pattern (Fig. 3). With the exception of the Sulawesi lowlands (70th percentile rank for amphibians), all other areas exhibited relatively high bird, mammal and amphibian endemism richness, highlighting relatively small differences in spatial patterns between taxonomic classes in areas of high LUI (Table S2).

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

DISCUSSION

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

Diverse global intensity patterns concordant with endemism richness are important as intensification processes are likely to have an array of effects on biodiversity (Donald *et al.*, 2001; Benton *et al.*, 2003; Kerr & Cihlar, 2004; Yamaguchi & Blumwald, 2005; Herzog *et al.*, 2008; Flynn *et al.*, 2009; Gibbs *et al.*, 2009; Kleijn *et al.*, 2009; Alkemade *et al.*,

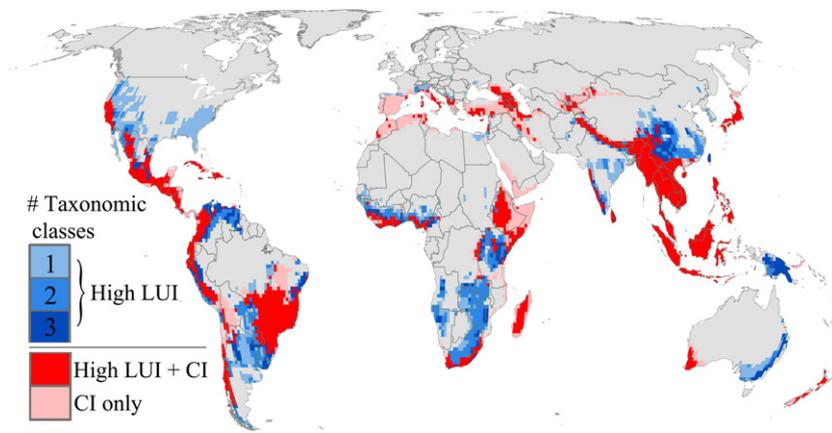


Figure 2 Regions of high land-use intensity (LUI) and high endemism richness for mammals, birds and amphibians from statistically significant ($P < 0.05$) local indicators of spatial association. Dark blue regions show high endemism richness for all three taxonomic classes associated with at least one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

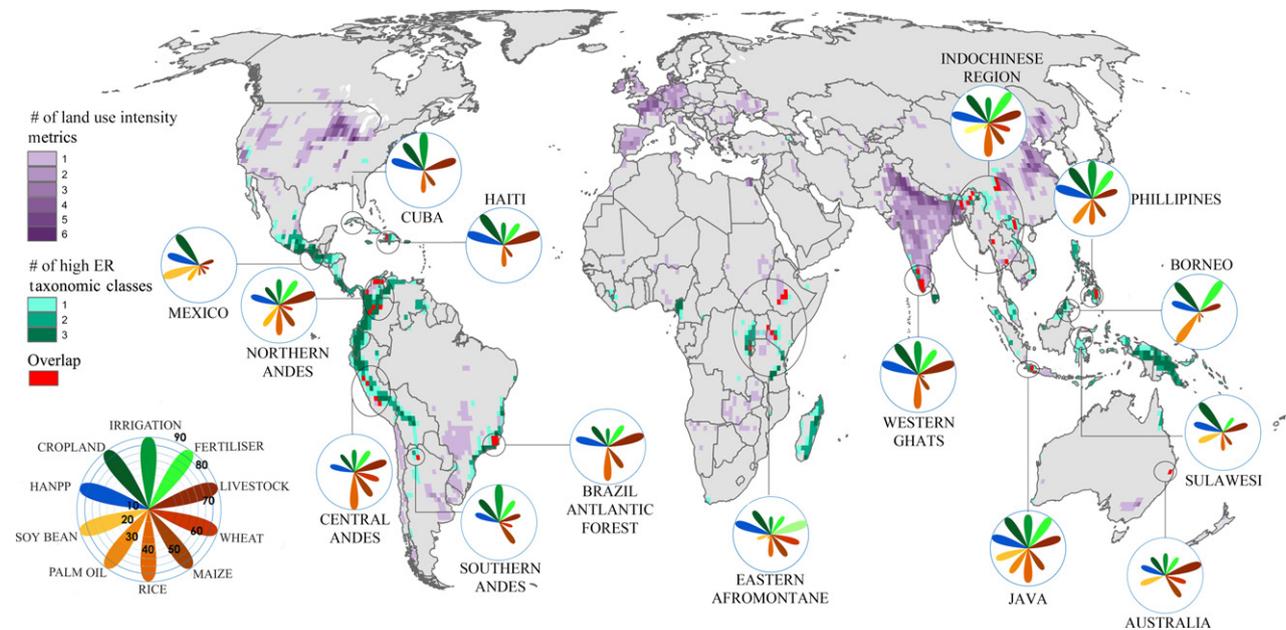


Figure 3 Top 2.5% of land-use intensity (LUI) and endemism richness, where any one top 2.5% intensity metric overlaps with any one top 2.5% of endemism richness (ER) for mammals, birds and amphibians, thus highlighting regions of particularly high pressure between human activity and wildlife (shown in red). Multiple overlapping LUI metrics of top 2.5% are shown in purple and multiple top 2.5% of endemism richness for taxonomic classes shown in turquoise. Numbers on the petal diagram represent percentile ranks for each LUI metric. Larger petals indicate higher percentile ranks and thus higher intensity of land use. Petals for input metrics are coloured in green, output metrics in orange and system metrics in blue. Percentile ranks for inverse yield gaps are given in Table S2 (Eckert IV projection, see online article for colour version).

2010, 2012; Felton *et al.*, 2010). Intensification processes are also likely to influence birds, mammals and amphibians in various ways. While broad patterns were overall remarkably similar, the results highlighted some differences in the detail. Unique taxon-specific areas associated with high LUI were highlighted for amphibians in the South-eastern USA, mammals in the Caucasus, amphibians and mammals in Europe and birds in Latin America and Australia. Such differences

among taxonomic classes are of interest as they suggest a limited usefulness of surrogate taxa on a global scale.

Of our thirteen LUI metrics, eight were related to the yield and yield gaps of different crops; therefore, it is not surprising that different patterns concordant with high endemism richness emerge. However, the differences that we found in high-intensity land use, not just between yields but also in the inputs involved in increasing yields, are diverse. We thus

highlight not only where different crops are grown intensively alongside biodiversity, but also the concordance of biodiversity and the high-intensity management processes behind such yields.

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

The incongruence of CI hotspots and regions of high LUI and high endemism richness further highlights this. Although the total area of high LUI and high endemism richness was slightly greater than the total area of CI hotspots, many large regions had no overlap. Considering the various negative effects intensification can have on biodiversity, such areas which were not covered by CI hotspots may merit more attention with a combination of relevant LUI metrics investigated accordingly. All regions where the top 2.5% of LUI and endemism richness overlapped were within CI hotspots. Thus, despite the incongruence of CI hotspots and regions of high LUI and endemism richness from the LISA analysis, when LUI is particularly intense (top 2.5%), the two distributions converge. This may, in part, be because in regions with particularly high LUI, some of the conditions used to define CI hotspots are met (e.g. 70% of native habitat lost). It should also be noted that the majority of the globe's land area (79%) was highlighted by one or more other global conservation priority schemes and that our regions of high LUI associated with high endemism richness are covered by several of these schemes (e.g. Papua New Guinea is included in High-Biodiversity Wilderness Areas, Venezuela and China by Megadiversity Countries and Eastern Africa by the Global 200 Ecoregions, see Brooks *et al.*, 2006).

In debates addressing broad topics such as sustainable intensification and biodiversity conservation, we recommend a more multidimensional approach to agricultural intensification, where relevant LUI metrics are included in accordance with research goals. Areas with high yield gaps and high endemism richness may represent potential future conflicts between high LUI and biodiversity. In less developed regions with high biodiversity, intensification can be limited by a lack

of capital investment and access to resources (Mueller *et al.*, 2012). However, foreign investment spurred by increasing land scarcity is increasing (Rulli *et al.*, 2013). For example, high cropland cover and HANPP now dominate in Southeast Asia, where the area of palm oil cultivation has increased by 87% in the last decade (FAOSTAT, 2010) and is one of the biggest threats to biodiversity in the region (Wilcove *et al.*, 2013). Considering the detrimental effects of using increased inputs such as fertilizer and pesticide on biodiversity (Kerr & Cihlar, 2004; Gibbs *et al.*, 2009), the various forms of intensification that are possible in these regions may result in considerable biodiversity threat and conservation conflicts. It should also be noted that areas shown here where future intensification may occur are based only on current low-intensity regions which may not necessarily become high intensity in the future due to many reasons such as poor soil quality, rugged topography or climate constraints.

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

We compiled a set of LUI metrics with the highest spatial resolution currently available. Nevertheless, despite considerable recent progress, numerous gaps exist regarding the availability of alternative indicators and the difficulties in their measurement related to issues with data availability, accuracy and error propagation (Kuemmerle *et al.*, 2013). With many inconsistent definitions in the literature, conceptually framing LUI is challenging (Kuemmerle *et al.*, 2013). Uncertainties in the accuracy of current LUI maps are often high due to inconsistent input data and limitations with processing algorithms and positional accuracy which is exacerbated by a lack of formal validation (Verburg *et al.*, 2011). Systematically collected ground-based data only cover a few regions of the globe, statistical data are often only available at the national scale, and remote sensing cannot easily capture the

subtle spectral effects of LUI changes (Kuemmerle *et al.*, 2013). Many LUI maps used here are based on one cropland hybrid map (Panel S1, Ramankutty *et al.*, 2008), and inaccuracies in the base map can propagate onto derivative maps (Verburg *et al.*, 2011; Table S1). This partly explains, for example, the large correlation found between fertilizer and cropland extent (0.92, Table S3). However, higher correlations were found between taxonomic classes, highlighting the variety in spatial patterns of LUI metrics.

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

In terms of biodiversity, we included just one global-scale measure. We chose endemism richness as it combines species richness and endemism (Fig. S8) and thus indicates the relative importance of a grid cell for species conservation on a global scale (Kier *et al.*, 2009). This is an advantage over species richness which is often representative of common, widespread species that can overshadow rare or small-ranged species, often in need of conservation (Grenyer *et al.*, 2006). Considering a more diverse range of biodiversity metrics may provide a richer view of patterns of LUI and biodiversity. However, as the main aim of this study was to compare the patterns of numerous LUI metrics concordant with biodiversity, and because a relatively large body of work has already been carried out on the differences between and the complexity of biodiversity metrics (Grenyer *et al.*, 2006; Kier *et al.*, 2009), we used only one measure of biodiversity. Future studies could consider a wider set of metrics, including information on abundance, functional, phylogenetic or beta-diversity. The inclusion of measures of ecosystem services, resilience, extinction debt (Essl *et al.*, 2015) and societal outcomes could also prove beneficial.

The paucity of readily available species occurrence data is a major impediment in mapping global patterns, with notably less data available for less charismatic species and less developed countries, which is where most biodiversity is thought to occur. High potentials for yield improvements are often found in lesser studied regions in the tropics (Mueller *et al.*, 2012), thus making the possible land-use threat to biodiversity even hazier. While species distribution data scaled to a finer resolution than 110×110 km are available, a substantial mismatch of global-scale range-map distributions with species' actual distributions occurs at finer scales, resulting in an overestimation of species occurrences (Hurlbert & Jetz, 2007). Therefore, at the current resolution, the exact configuration of land uses within each grid cell cannot be accounted for. This resolution is also likely to oversimplify fine-scale patterns of concordance of LUI and biodiversity, and differences between taxonomic classes. This has implications for what is in reality a LUI-biodiversity

hotspot but has been missed as a hotspot due to taking the average LUI values per grid cell; that is, a grid cell may contain both very high and very low LUI but is represented here as medium LUI due to averaging. Furthermore, the same data can produce different results when aggregated in different ways – this is applicable to any zoning of spatial units and is known as the modifiable areal unit problem (Openshaw & Taylor, 1979; Jelinski & Wu, 1996). Together, these issues represent limitations for studying the effect of LUI on biodiversity.

CONCLUSIONS

Considering the increasing demand for food and bioenergy production, understanding the pressure land-use change exerts on biodiversity is crucial. In the past, such assessments have predominately focused on the extent of land use. However, intensification has been a major mode of land-use change historically (Rudel *et al.*, 2009) and is likely to continue due to economic pressure and government policies to intensify agriculture in less developed, yet highly biodiverse areas (van Vliet *et al.*, 2012). Different LUI metrics highlight different high-pressure regions, suggesting conservation research should embrace the multiple aspects of LUI and include relevant intensity metrics when considering biodiversity threat. This is particularly important as most global assessments of the land-use impact on biodiversity, as well as the current land sparing vs. land sharing debate, have at best relied on single measures of LUI (Ellis & Ramankutty, 2008; Kleijn *et al.*, 2009; Pekin & Pijanowski, 2012). We identify areas of particularly high endemism richness and high LUI and thus shed light on regions of potential conflict where highly intensive agriculture and unique biodiversity coincide.

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

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SUPPORTING INFORMATION

Additional Supporting Information may be found in the online version of this article:

Panel S1 Bibliography of datasets used for Endemism Richness and LUI metrics.

Table S1 Details on datasets of LUI metrics.

Table S2 Average percentile ranks for LUI and Endemism Richness in top 2.5% hotspots.

Table S3 Spearman's rank correlation coefficients of LUI, Endemism and Species Richness datasets.

Figure S1 Top 2.5, 5, and 10% of LUI metrics.

Figure S2 Top 2.5, 5, and 10% of Endemism Richness.

Figure S3 Individual LISA results for each LUI metric and Endemism Richness.

Figure S4 (a) Areas of low Endemism Richness and high LUI and (b) high Endemism Richness surrounded by low LUI areas according to statistically significant ($P < 0.05$) LISA results.

Figure S5 Percentage of ecozone containing regions of high Endemism Richness and high LUI from LISA analysis ($P < 0.05$).

Figure S6 Areas where high LUI (combined for input, output and system metrics) are associated with high Endemism Richness (for each taxonomic class) from LISA analysis.

Figure S7 Regions of high land-use intensity (LUI) and high endemism richness compared to CI hotspots.

Figure S8 Endemism Richness for mammals, birds and amphibians.

BIOSKECTHES

Laura Kehoe is a PhD student currently interested in how consumption and human population growth rates can drive land-use change and how this in turn can influence biodiversity.

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