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The role of global dietary transitions for safeguarding biodiversity

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Roslyn C. Henry^{a,*}, Peter Alexander^{a,b}, Sam Rabin^c, Peter Anthoni^c, Mark D.A. Rounsevell^{a,c}, Almut Arneth^c

^a School of Geosciences, University of Edinburgh, Drummond Street, Edinburgh, EH8 9XP, United Kingdom

^b Global Academy of Agriculture and Food Security, The Royal (Dick) School of Veterinary Studies and The Roslin Institute, University of Edinburgh, Easter Bush Campus, Midlothian, EH25 9RG, United Kinedom

^c Karlsruhe Institute of Technology, Institute of Meteorology and Climate Research / Atmospheric Environmental Research, Garmisch-Partenkirchen, Germany

through dietary change.

| ARTICLE INFO | A B S T R A C T |
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| Keywords: Biodiversity Land use change Diet Consumption | Diets lower in meat could reduce agricultural expansion and intensification thereby reducing biodiversity im- pacts. However, land use requirements, associated with alternate diets, in biodiverse regions across different taxa are not fully understood. We use a spatially explicit global food and land system model to address this gap. We quantify land-use change in locations important for biodiversity across taxa and find diets low in animal products reduce agricultural expansion and intensity in regions with high biodiversity. Reducing ruminant meat consumption alone however was not sufficient to reduce fertiliser and irrigation application in biodiverse lo- cations. The results differed according to taxa, emphasising that land-use change effects on biodiversity will be taxon specific. The links shown between global meat consumption and agricultural expansion and intensification in the biodiverse regions of the world indicates the potential to help safeguard biodiverse natural ecosystems |

1. Introduction

Expansion of agricultural land, together with intensified management practices are some of the greatest threats to the conservation of terrestrial ecosystems and biodiversity (Machovina et al., 2015; Machovina and Feeley, 2014; Marchal et al., 2011; Newbold et al., 2015; Ripple et al., 2014a). Over 35% of the Earth's permanent ice-free land surface is currently used for food production (Foley et al., 2005), with the expansion of agricultural land for food production in the last 300 years estimated to have reduced natural grasslands by up to fifty percent and natural forests by one third (Klein Goldewijk et al., 2011). The associated loss of natural ecosystems has had negative consequences for biodiversity (Gibson et al., 2011; Pereira et al., 2012; Pimm et al., 2014). Agricultural intensification that increases yields can reduce the area of land needed for production, but can also harm biodiversity through fertiliser and pesticide pollution (Flohre et al., 2011; Gibbs et al., 2009; Kleijn et al., 2009) as well as impact on river flows through abstraction of water for irrigation (De Frutos et al., 2015; Yamaguchi and Blumwald, 2005). Land-use change models have demonstrated that biodiverse regions will be significantly threatened by future agricultural expansion and intensification (Delzeit et al., 2017; Kehoe et al., 2017, 2015). Protected areas can be an effective

contribution to prevent agricultural expansion (Pringle, 2017), but conservation efforts that focus on food demand will also play a role.

Meat production has been associated with higher land and water use, and higher greenhouse gas (GHG) emissions, per unit of energy or protein than other foods (Machovina et al., 2015; Poore and Nemecek, 2018; Tilman and Clark, 2014a). In particular, heavily managed and densely stocked pastures pose serious threats to biodiversity (Machovina and Feeley, 2014; Ripple et al., 2014a). 65% of agricultural expansion in recent decades has been associated with increased production of animal products (Alexander et al., 2015), and land-use changes associated with animal husbandry account for roughly 30% of current global biodiversity loss (Westhoek et al., 2011). Livestock production is increasing most rapidly in tropical regions with high biodiversity (Machovina et al., 2015). The tropics are also experiencing the highest rates of species extinction (Dirzo et al., 2014), at a time when global extinction rates have been estimated to be 1000 times the geological background rate (Pimm et al., 2014, 1995). Much future human population growth is expected to occur in these biodiverse tropical nations, and as incomes continue to rise in developing countries, animal product consumption is expected to increase further (Machovina et al., 2015; Stoll-Kleemann and Schmidt, 2017). If current trends in animal product consumption continue, and if industrialised

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^{*} Corresponding author at: Roslyn C Henry, School of Geosciences, University of Edinburgh, Drummond Street, Edinburgh, EH8 9XP, United Kingdom. *E-mail address:* roslyn.henry@ed.ac.uk (R.C. Henry).

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countries do not reduce high rates of meat consumption, it is estimated that one billion additional hectares of natural land will be cleared for agriculture by 2050 (Tilman et al., 2011, 2001).

Reducing meat consumption would not only improve global human health-consumption of meat in industrialised countries is currently double the amount that is deemed healthy (Wellesley et al., 2015)-but the Intergovernmental Panel on Climate Change (IPCC) also identified it as an important focus for climate change mitigation (de Coninck et al., 2011). Modelling studies have quantified land-use changes associated with dietary shifts, demonstrating that demand-side reductions in meat consumption could reduce GHG emissions and deforestation (Bajželj et al., 2014; Erb et al., 2016; Popp et al., 2010; Stehfest et al., 2009: Tilman and Clark, 2014a: Wirsenius et al., 2010). However, fewer studies (Kok et al., 2018; Tilman et al., 2017; Visconti et al., 2016) have considered the effects of diet on biodiversity, and none have explored the spatial impacts across multiple taxa. The spatial nature of biodiversity and variations in distributions between taxa means that spatially explicit analyses are required to understand the impact of dietary choices on biodiversity.

Here we address this critical gap in understanding the environmental consequences of food-system changes. We use a global foodsystem model (PLUMv2/LPJ-GUESS, Alexander et al., 2018) to explore land use and agricultural intensity change until 2100 under three alternative dietary scenarios: Business-as-usual (BAU), 95% reduction in ruminant product consumption (LOW-R), 95% reduction in animal product consumption (LOW-R). This work is unique in considering the spatially disaggregated consequences of future dietary scenarios for high biodiversity locations across different taxa. We also, for the first time, consider nitrogen fertiliser application and irrigation intensity changes in locations important for biodiversity.

2. Methods

2.1. Modelling framework

PLUMv2 is a global land use and food-system model that combines spatially-explicit, biophysically-derived yield responses with socioeconomic scenario data to project future demand, land use, and management inputs (Alexander et al., 2018). For each country and timestep, the agricultural land use and level of imports or exports is determined through a least-cost optimisation that meets the demand for food and bioenergy commodities in each country. Food demand is projected based on log-linear relationships with per-capita income using GDP and populations from the Shared Socioeconomic Pathway (SSP) scenarios (O'Neill et al., 2014). Demand for food and bioenergy commodities is projected at a country level for six commodity groups: cereals, oilcrops, pulses, starchy roots, ruminant products, and monogastric products. Demand for dedicated energy crops (i.e., secondgeneration bioenergy) is specified as a global trajectory with all production locations determined endogenously. Food and bioenergy demand are met by in-country expansion or intensification of crops or from imports from the global market. Commodities produced in excess of a country's domestic demand are exported to the global market. The global market is not constrained to be in equilibrium, instead allowing over or under supply of commodities buffered through modelled stocks. Prices are updated for the next year based on the aggregate inbalance of imports and exports in that year. For example, over supply of a commodity on the global market decreases the price; this reduces the benefits from its export and reduces the cost of importing it, creating a tendency to correct for the oversupply. For each commodity a single tariff free price exists in each time step, which is adjusted for transport costs and other barriers, e.g. tariffs, to obtain country specific prices.

Crop yield responses for the seven crops (wheat, maize, rice, oilcrops, pulses, starchy roots, energy crops) used in PLUMv2 are provided on a 0.5° grid by a dynamic global vegetation model, LPJ-GUESS (Olin et al., 2015; Smith et al., 2014), for a range of fertilisation rates and rain-fed vs irrigated conditions. Other management practices (e.g. pesticide application, mechanical equipment, reseeding of grassland) are represented in PLUMv2 by a "management intensity" factor. Land use associated with crops that are not explicitly modelled is accounted for through an unhandled crop adjustment rate. Using FAO data we calculate the percentage of land currently accounted for by crops we do not model (~17%). We then use this as a rate to calculate the additional cropland area that would be required if we included other crop types, which is added to the cropland calculated by the land use optimisation process. Therefore, with any change in cropland area, the production of all plant food is scaled. Natural land cover here is comprised of forested natural land, non-forested natural land and abandoned agricultural land. In the grid cells, four decision variables (area, fertiliser, irrigation, and other intensity) for each of the eight land use types (seven crop types plus pasture) are determined during the optimisation. To determine land use solutions that meet country level demand in the optimisation step, PLUMv2 uses the spatially specific crop yield responses to intensity inputs, various land use costs (such as land conversion costs and input costs), and trade costs.

Socioeconomic parameters, population trajectories and GDP trajectories are in line with the "middle of the road" SSP scenario (SSP2), with trends largely exhibiting historic patterns (Dellink et al., 2017; Jones and O'Neill, 2016). The SSPs describe alternative global societal pathways through the 21st century (O'Neill et al., 2015, 2014).

Population and GDP trajectories are taken from SSP2 using World Bank projections (IIASA, 2014). Historical demand for food commodities is taken from FAOSTAT to parameterise projections of future food demand (FAOSTAT, 2015a, 2015b). The climate and atmospheric CO₂ forcing scenario RCP 6.0 is used as it is considered the Representative Concentration Pathway (van Vuuren et al., 2011) most consistent with SSP2 (Engström et al., 2016). Forcings are taken from the 1850-2100 IPSL-CM5A-MR outputs from the Fifth Coupled Model Intercomparison Project (CMIP5). First- and second-generation bioenergy demand trajectories are specified exogenously to represent a business-as-usual scenario with no specific climate change mitigation policies. Demand for first-generation bioenergy is modelled from an observed baseline level of demand (Alexander et al., 2015; FAOSTAT, 2015a) adjusted to double by 2030 from the 2010 level and thereafter remain constant. Global demand for dedicated second-generation bioenergy crops increases to 4000 Mt DM/year by 2100, in line with the SSP2 demand with baseline assumptions (Popp et al., 2016). For parameter settings that are not specified exogenously from available data on existing and future trends, for example technology change rates, we use expert judgement to align quantitative parameter settings with the qualitative SSP2 storyline. Scenario elements of the SSP2 narrative that are assumed to influence changes in the PLUMv2 input parameters are identified. Qualitative changes in parameters are estimated based on an interpretation of the SSP2 storyline (Engström et al., 2016). These qualitative estimates of parameters and uncertainty levels are translated into quantitative values characterised by a uniform distribution. Each parameter therefore has a range defined by 50% above and below the central parameter values. A Monte Carlo approach to explore uncertainty associated with input parameters is used and parameters are sampled using a Sobol sequence method with n = 30 (Chalaby et al., 2015); the central parameter values used in each of the scenarios can be found in Appendix C, Table C2. This approach allows us to capture the uncertainty within the model framework.

2.2. Protected areas

The proportion of protected land with a status of "designated" and IUCN category I–VI within a grid cell is calculated using the WDPA database (UNEP-WCMC, 2016). Within each grid cell, natural land designated as protected is prevented from conversion to any form of agricultural use. Within each grid cell, a minimum fraction (5%) of primary unprotected natural land is also prevented from agricultural

use due to assumed limits to agricultural production, e.g. field boundaries, roads/tracks, and other farm infrastructure. Slope constraints (IIASA/FAO, 2010) also prevent agricultural use in regions of high altitude. In cases where agricultural land already exceeds the area specified as protected, no further agricultural expansion can occur. China's National Forest Protection Program is implemented as an annual limit to deforestation of 1.1% in China (Ren et al., 2015).

2.3. Scenario description

2.3.1. Business as usual (BAU)

The business as usual scenario scenario assumes that the shift in consumption away from staples, such as pulses and starchy roots, and towards animal products continues as incomes rise. The relationship between rising income and increasing consumption of commodities such as meat, milk, and refined sugars has been observed historically; therefore, in line with the SSP2 pathway, we assume future consumption trends in the baseline largely exhibit historic patterns (Keyzer et al., 2005; Tilman et al., 2011).

2.3.2. 95% reduction in ruminant product consumption (LOW-R)

The 95% reduction in ruminant product consumption scenario represents a major shift in world consumption patterns of ruminant products, which could be potentially driven by increasing meat prices induced by stricter climate and health policies, consumer awareness, and increasing land and animal feed expenses. This scenario assumes that the consumption of ruminant products decreases steadily from 2010 to 2100 until crop products replace 95% of ruminant product consumption. Ruminant products are replaced by a mixture of cereals, starchy roots, pulses, and oilcrops; however, the same calorie intake is maintained. An example of the dietary changes in terms of per capita consumption and the proportions of substitution are given in Appendix C, Table C1 and Table C2 respectively. 95% was chosen for the stylised scenarios to demonstrate the potential effects a very large, but not total, reduction in ruminant product consumption would have on global land use.

2.3.3. 95% reduction in animal product consumption (LOW-AP)

The 95% reduction in animal product consumption scenario is similar to the above, but assumes that non-meat commodities replace both ruminant and monogastric consumption.

2.4. Exploring the consequences of dietary change for biodiversity

2.4.1. Conservation International (CI) biodiversity hotspots

The 35 CI hotspots cover 2.3% of the land surface but support 50% of the world's endemic plant species and 43% of vertebrate endemic species. To qualify as a hotspot, a region must be threatened —i.e. contain at most 30% of its original natural vegetation—yet contain at least 1500 endemic vascular plants. The CI biodiversity hotspot database is used to identify particular regions of importance for biodiversity (Mittermeier et al., 2004; Myers et al., 2000). CI hotspot shapefile data are converted to 0.5° raster maps. Any 0.5° cell containing CI hotspot polygon data is classified as a CI hotspot irrespective of hotspot size. The CI map is therefore binary and cells are classified as either a CI hotspot or not.

2.4.2. Vertebrate species richness maps

Criteria for the CI biodiversity hotspots database only account for vascular plant species richness. Thus, we also consider maps of vertebrate species richness, small-range vertebrate species richness, and threatened species richness (Jenkins et al., 2013; Pimm et al., 2014). The resolution of the vertebrate species richness maps was decreased from 0.1° to 0.5° resolution to match PLUMv2; the mean species richness was calculated for each grid cell. For all taxa, the distribution of species richness across grid cells is right-skewed: most cells contain a

few species while there are a few cells with a large number of species. For each taxon's map we therefore convert the mean species richness values of grid cells into percentile values (richness index). We assume that 'species-rich regions' comprise cells with a richness index ≥ 0.9 , i.e. the 90th percentile of grid cells and therefore, similar to the CI hotspots, we focus on those regions with the greatest biodiversity (appendix A, figures A1-3).

We explore land use change, agricultural expansion, and intensification projected by PLUMv2 in CI hotspots and in vertebrate species-rich regions for the different dietary scenarios. We consider the loss of natural land, forests, and natural grasslands and changes in input intensities such as fertiliser and irrigation in grid cells classed either as CI hotspots or with a richness index ≥ 0.9 . From this, we identify regions of threat using a threat index: regions with high biodiversity that overlap with areas of projected agricultural expansion. We calculate this overall threat index for all species in each 0.5° grid cell. This is the proportion of natural land projected to be lost by 2100 multiplied by the summed richness index of birds, mammals, and amphibians for the median PLUMv2 parameter simulation run. For the threat index we therefore assume each species is equally important regardless of taxon.

3. Results and discussion

3.1. Land cover change in biodiverse regions

In agreement with results from previous modelling studies (Delzeit et al., 2017; Kehoe et al., 2017, 2015), the most threatened regions-locations with high biodiversity under pressure from agricultural expansion-are in the tropics under BAU scenarios (Fig. 1). Scenarios of lower animal product consumption (LOW-R and LOW-AP) greatly reduce agricultural expansion in regions of high biodiversity compared to the BAU scenario (Fig. 1 and 2). By 2100 under BAU 9% (984 Mha) of global natural land is lost, of which 95% is in the tropics-equivalent to 24% of natural land in these latitudes (Fig. 2). Conversely, reduced animal product consumption (LOW-AP) results in a 7% (703 Mha) increase in global natural land between 2010-2100 (Fig. 2, Appendix B Figure B1) with lower losses across the tropics (Figs. 1 and 2) and increases in natural land across the northern hemisphere (Fig. 2). Deforestation and land clearing for agriculture have been identified as the leading causes of biodiversity decline (Gibson et al., 2011). Therefore, the potential for dietary change to reduce global agricultural land area by approximately 1687 Mha by 2100 (11% of global land area when comparing BAU to LOW-AP) is an important finding for biodiversity conservation (Laurance et al., 2012; Pereira et al., 2012).

Species-rich regions across the different taxa are largely found in the tropics (Appendix A, Figure A1-3) and the greatest loss of natural land in species-rich regions occurs in BAU (Fig. 3). In BAU, on average, 98% of global pasture expansion takes place in the tropics as demand for ruminant products in tropical countries increases with increasing population and income (Appendix C, Figure C2). As incomes increase, consumption shifts from staples such as starchy roots and pulses to commodities such as meat, milk, and refined sugars (Keyzer et al., 2005; Tilman et al., 2011). However, the rate of increasing consumption of animal products slows and plateaus with any further rise in income (Cole and Mccoskey, 2013), which is also represented in the log-linear relationships with per-capita income used in our model (Alexander et al., 2018). Consequently, in developing tropical countries, the transition from low incomes to high incomes results in greater demand of ruminant products (Appendix C, Figure C2), and pasture expands at the expense of natural land. In contrast, income and the animal product consumption in developed countries outside the tropics are already high, with large areas of existing pasture meeting demand for ruminant products. Given the relationship between income and consumption, increases in income in developed countries do not lead to further large increases in demand for animal products (Appendix C,



Fig. 1. Spatial distribution of regions of threat; regions with high biodiversity under pressure from agricultural expansion. The left column (a,c,e) is the BAU scenario and the right column (b,d,f) is the LOW-AP scenario for the different types of species richness. Blue dashed lines delineate the tropics. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article).

Figure C2). Under LOW-AP and LOW-R, abandonment of existing pasture in developed countries leads to large increases of natural land at a global level (Fig. 2). This does not coincide with large increases in natural land in species-rich regions (Fig. 3), however, because it largely takes place in locations that are not here classified as species-rich — i.e. those outside the tropics. This result can be seen when comparing Figures A1–A3 in Appendix A (spatial distribution of species-rich regions for the different taxa) with Fig. 2. In species-rich regions the LOW-R and LOW-AP scenarios reduce pasture expansion rather than increase natural land. Although existing pasture in the tropics is also abandoned, this is offset by cropland expansion (see below); therefore natural land area in species-rich regions under LOW-R and LOW-AP is relatively stable compared to BAU (Fig. 3).

Cropland expands by 28% in the tropics under BAU to produce crops for food and as animal feed as demand for animal products grows in the developing world. Under LOW-R, cropland expands by 38% in the tropics; this is greater than under BAU because demand for food and feed for monogastrics is the same while additional crops are required to replace ruminant products. Under LOW-AP, despite reduced demand for feed for animals, existing cropland area in 2010 is not sufficient to produce enough crops to replace animal products and meet food demand of a growing population; consequently, cropland still expands by 27%. The greater cropland requirements under LOW-R explain the marginally greater losses of natural land in species-rich regions (Fig. 3) in LOW-R compared to LOW-AP. However, on average, the amounts of water and nitrogen applied to cropland in the tropics under LOW-AP are 42% and 68% less, respectively, than under BAU. Therefore, while the total area of cropland remains the same in the tropics, the intensity of agricultural inputs declines under LOW-AP with the reduction in demand for animal feed.

Tilman et al. (2017) investigated the biodiversity of mammals and birds in a non-spatial, country-level approach and found dietary change reduced extinction risk. Previous spatially explicit studies typically only consider single taxon with amphibians particularly underrepresented. For example, Visconti et al. (2016), considering mammals, found consumption change could reduce extinction risk. The locations classified here as species-rich differ between mammals, birds and amphibians (see Appendix A, Figures A1-3). Differences regarding the impacts of land-use change therefore arise between and within taxa, and are important when considering conservation targets (Ceballos and Ehrlich, 2006; Jenkins et al., 2013; Orme et al., 2005; Pimm et al., 2014; Possingham and Wilson, 2005). For example, natural land loss in parts of Ecuador overlap to a greater extent with regions of threatened bird species-richness than with regions of threatened mammal-speciesrichness. While broad patterns are similar across CI hotspots and taxa-for example, the greatest loss of natural land occurs in BAU while the LOW-R and LOW-AP scenarios result in smaller losses or increasing natural land cover (Fig. 3)-important differences remain owing to the different distributions of the species groups. For example, with LOW-AP, while the small ranged species-rich regions shows little change or

(a) BAU natural land fraction change 2010-2100





(c) LOW-R natural land fraction change 2010-2100

-0.6



Fig. 2. Change in natural land cover fraction between 2010-2100 for (a) BAU (b) LOW-AP (c) LOW-R. Dotted lines delineate the tropics.

decreases in natural land cover by 2100, the grid cells within the threatened species-rich region show increasing natural land cover by 2100. Changing dietary patterns may therefore have the greatest benefits for regions containing threatened species in term of habitat recovery. Measures of total species richness are important when considering threats to overall range size and ecosystem functioning related to population sizes. However, the richness of small-ranged species and/ or threatened species are often regarded as more appropriate measures

when planning conservation to prevent extinctions (Ceballos and Ehrlich, 2006). Visconti et al. (2015), for example, highlighted the importance of considering the status of taxa from a protected area perspective: Targeting protection towards threatened species had positive effects on suitable habitat for terrestrial mammals, while expanding protected areas according to ecoregion targets had negative effects. Furthermore, a number of studies have demonstrated that hotspots of species richness between taxa and classifications of taxa are



Fig. 3. Projected natural land change by 2100 in.(a) bird-, (b) mammal-, and (c) amphibian- species-rich regions, and (d) CI hot-spots for the different dietary scenarios. Species-rich regions are comprised of cells with a richness index ≥ 0.9 . Colours in a-c represent the different types of species-rich regions: all species (blue), small-ranged species (orange), and threatened species (red). Boxplots distributions generated with n = 30. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article).

All species Small range species Threatened species

often incongruent (Jenkins et al., 2013; Orme et al., 2005; Pimm et al., 2014). The differences between CI hotspots and type of taxa here further support the argument that no single metric is sufficient when considering threats to, and the conservation of, biodiversity (Ceballos and Ehrlich, 2006; Jenkins et al., 2013; Orme et al., 2005; Pimm et al., 2014; Possingham and Wilson, 2005).

3.2. Agricultural intensity change

The type and level of agricultural management has an important role in the impact on different taxa (De Frutos et al., 2015; Flohre et al., 2011: Gibbs et al., 2009: Kleiin et al., 2009: Yamaguchi and Blumwald, 2005). For example, at a European scale Flohre et al. (2011) found that while agricultural intensity negatively affected the species richness of birds, it did not affect carabid beetles. Increasing nitrogen reduces plant biodiversity (Bobbink et al., 2010; Reich, 2009; Stevens et al., 2004) with consequences for faunal biodiversity (Nijssen et al., 2017). Bobbink et al. (2010) highlighted that the negative effects of nitrogen accumulation on biodiversity has occurred across a wide range of ecosystems and geographic areas while Nijssen et al. (2017) identified ten pathways through which increased nitrogen alters faunal biodiversity. N-driven faunal decline has been demonstrated, for example, in some rare bird species where elevated nitrogen application reduced vegetation heterogenity and/or preferred habitat with consequences for prey abundance (de Vries et al., 2011). However, there remain knowledge gaps regarding the mechanisms that drive observed biodiversity changes. Similarly, there is a body of evidence that demonstrates the negative effects of water extraction on natural ecosystems, with 70% of freshwater withdrawal globally used in agriculture (FAO, 2016). The disruption of water flows and river regulation has, for example, altered floodplain forests resulting in their dieback globally. Such forests are ecologically important due to their high biodiversity, with climate change induced droughts likely to further exacerbate forest mortality (Horner et al., 2009). Furthermore, intensive livestock farming that uses irrigation and involves irrigation return flows has also been found to substantially alter water chemistry of nearby rivers with potential consequences for both aquatic and riparian species diversity (Martín-Queller et al., 2010). Given the implications for biodiversity of increasing nitrogen and irrigation use the need to consider such consequences are apparent. However, no previous land use modelling studies have explored changes in irrigation and nitrogen fertiliser intensities that are associated with reductions in meat consumption in biodiverse regions. Agricultural intensity is typically represented in land-use models in a stylised and spatially aggregated manner, making the evaluation of their impacts challenging (Lotze-Campen et al., 2008; Nelson et al., 2014). Our analysis addresses this gap and by including spatially specific crop responses to different inputs in our modelling framework. We are able to show the effects of dietary changes on input intensity, with a focus on species-rich-regions where biodiversity impacts are likely to be most acute.

In the LOW-R scenario, demand for monogastric feed crops is unchanged from BAU, while demand for food crops increases to replace ruminant products (Appendix C, Figure C1). This net increase in crop demand results in crop area expansion relative to BAU. However, the median increase in nitrogen and irrigation, in CI hotspots and speciesrich regions, under LOW-R are similar to BAU (Figs. 4 and 5). LOW-AP decreases demand relative to BAU for monogastrics, as well as ruminants, and consequently decreases demand for crops as feed (Figure C1). Rather than reduce cropland area, this results in reduced nitrogen and water inputs in these locations. Reduced feed production therefore has the greatest potential to reduce inputs, and replacing pasture-fed ruminant products alone may not have substantial benefits for biodiversity in terms of species affected by fertiliser and irrigation..

The differences in nitrogen and water inputs between alternate dietary scenarios highlight the need to consider fertiliser and irrigation individually. Any potential intensity changes associated with dietary change will require scrutiny as measures to reduce agricultural expansion may not necessarily reduce intensification. We do not consider a scenario with a 'livestock revolution'-a shift away from pasturebased production toward industrialised production that requires cropbased feeds (Delgado et al., 2001; Naylor et al., 2005; Swain et al., 2018)—which could similarly reduce the rate of agricultural expansion, but with increased intensity. There is an inherent trade-off between agricultural intensification and expansion. Intensification is more polluting, but requires less land, while expansion is less polluting, but requires more land. Ultimately, both can have negative consequences for biodiversity and thus managing this trade-off is complex. For example, the recent IPBES Regional Assessment for Europe & Central Asia recommends that Europe reduce agricultural intensity to conserve European biodiversity (IPBES, 2018). However, this could displace food production and the associated consequences for biodiversity, through imports, to other parts of the world.

Within scenarios, the intensity results show large differences across species-rich regions, establishing the need to consider land expansion jointly with land management when assessing biodiversity impacts of land-use change, and to provide these analyses for individual taxa of different status. For example, increases in irrigation water applied in locations rich in small-ranged amphibians are greater compared to locations rich in small-ranged birds or mammals (Fig. 4). Without separating out taxa, such a finding could be overlooked, despite the probable greater importance of irrigation water withdrawal for amphibian populations. The intensity change results are heterogeneous between the different regions of species richness because food demand, the crops grown, and yield response to agricultural inputs are locationspecific (see methods). We find, for example, nitrogen and irrigation application in bird-species-rich regions increases over the period 2010-2100 (Fig. 5a). Conversely, nitrogen and irrigation application decline in threatened mammal- and amphibian-species-rich regions. In the threatened mammal and amphibian locations by 2100 under BAU, agricultural area expands (Fig. 3) to meet demand. This expansion reduces the need for intensification such that less nitrogen and water are required. In the LOW-AP scenarios, in the threatened mammal and amphibian locations, agricultural areas shrink as nitrogen and water use decrease (Fig. 3). Changing dietary demand may therefore have the greatest benefits for threatened species through the reduction of both agricultural land area and agricultural inputs in regions of high biodiversity.

3.3. Uncertainty and limitations

The stylized scenarios here assume high substitution rates of animal products, 95%, similar to other studies that have assumed shifts towards complete vegetarianism (Stehfest et al., 2009; Tilman and Clark, 2014a) or large reductions in animal products. For instance, Visconti et al. (2016) assumed reducing meat and egg consumption in all regions by 76-88%. Such scenarios are useful for illustrating the effects of dietary transitions on land use changes. Steps towards more sustainable diets will first require globally more equitable consumption of animal protein and thus large scale reductions of meat consumption may only be appropriate in parts of the world that are overconsuming meat. However, arguably such large scale shifts will face barriers as dietary choices are influenced by a number of factors such as health, culture, price, availability, taste, and convenience. Taking such factors into account may reduce the potential for large scale dietary change. Lower rates of animal product substitution would inevitably result in lower environmental benefits in this study and others. In general in all studies the degree of animal product consumption is strongly linked to land use and GHG emissions with higher rates of meat consumption reduction being more beneficial for the environment (Hedenus et al., 2014; Stehfest et al., 2009).

We explore land use change in regions with the greatest levels of biodiversity by including CI hotspots and grid cells that are in the 90th



Fig. 4. Projected change in irrigation water use by 2100 in.(a) bird-, (b) mammal-, and (c) amphibian-species-rich regions and (d) CI hotspots for the different dietary scenarios. Species-rich regions are comprised of cells with a richness index \geq 0.9. Colours in a-c represent the different types of species-rich regions: all species (blue), small-ranged species (orange), threatened species (red). Boxplots distributions generated with n = 30. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article).

All species Small range species Threatened species

percentile for species richness in our analysis, thus focussing the analysis on tropical regions. Using absolute species richness to identify regions for our analysis has the advantage of highlighting today's highly biodiverse regions at risk, with land use change in these areas potentially having a disproportionate effect on global biodiversity loss.

Similar to other studies we find these highly diverse regions, such as sub-Saharan Africa and Latin America, are suitable for large scale agricultural expansion, further highlighting their importance in terms of conservation. However, the focus on areas with the highest biodiversity inevitably means the consequences for biodiversity temperate or



Fig. 5. Projected nitrogen fertiliser intensity change by 2100 in.(a) bird-, (b) mammal-, and (c) amphibian-species-rich regions and (d) CI hotspots for the different dietary scenarios. Species-rich regions are comprised of cells with a richness index \geq 0.9. Colours in a–c represent the different types of species-rich regions: all species (blue), small-ranged species (orange), threatened species (red). Boxplots distributions generated with n = 30. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article).

[⇒]All species ⇒ Small range species ⇒ Threatened species

other climate zones are under-represented by our approach. Globally changing dietary patterns do affect temperate regions in our analysis. For example reducing animal product consumption increases natural land across the northern hemisphere (Fig. 2). While these regions do not necessarily harbour high levels of biodiversity, and are therefore not in our 90th percentile, they nevertheless contain species of significant conservation or cultural importance. Therefore, while it was out of the scope of our study to consider all geographic regions, temperate zones should not be overlooked.

Land use changes to meet demand in PLUMv2 arise through a complex decision making process that involves assessing spatially explicit crop yield responses, a variety of agricultural costs and trade related costs. The parameter settings used in this study produced benchmarking results in line with historical data (Alexander et al., 2018). However, agricultural costs may change with future economic development and policies. The assumptions regarding future socioeconomic and climate condition are based on SSP2 and RCP 6.0 respectively. Further analysis under a range of SSP trajectories may alter the land use patterns we find. For example, changing GDP, population size, or bioenergy demands (such as increasing bioenergy under SSP1) would alter the baseline food and energy demand projections and change supply requirements with consequences for land use. SSPs that therefore project more food and energy demand than SSP2 used here, particularly in developing tropical countries, will likely result in greater agricultural expansion in biodiverse regions. Similarly, alternative climate pathways may have consequences for projected intensity use in biodiverse regions. Increased atmospheric CO2 levels are linked to higher yield potentials, reduced nitrogen losses and greater water use efficiency. In previous work this leads to lower fertiliser and irrigation inputs in PLUMv2 (Alexander et al., 2018). Therefore, while lower climate forcings could be beneficial for climate change, they may have unexpected negative effects such that more inputs are required in agriculture to achieve desired vields to meet demand. Changing both the SSP and RCP trajectory used in modelling studies of biodiversity may therefore alter the spatial patterns of threats to biodiversity. Indeed recent modelling studies comparing SSPs and RCPs found that stronger mitigation scenarios, corresponding to lower RCPs, had greater benefits for biodiversity (Chaudhary and Mooers, 2018; Newbold et al., 2015).

3.4. Conclusions and perspectives

We find diets low in animal products reduce agricultural expansion and intensity in regions with high biodiversity and that the magnitude of change differed according to taxa, emphasising that land-use change effects on biodiversity will be taxon specific. Numerous tropical countries with high biodiversity have rates of increasing per capita meat production, and several are projected to require up to 30% more agricultural land by 2050 (e.g. Ecuador, Brazil, and China) (Machovina et al., 2015). Our results also demonstrate the importance of developing countries, particularly those in the tropics, for biodiversity. The transition from low incomes to high incomes and the associated increase in animal product consumption in developing countries drives large losses of agricultural land across the tropics and in species-rich-regions under BAU. In many developing countries, access to sufficient protein is limited and demand-side measures such as global dietary interventions could be detrimental to the welfare of populations and thus not ethical. Efforts to preserve biodiversity and ecosystem functioning will therefore require scrutiny to ensure that changes are complementary to food security goals in developing countries (including nutritional requirements) and respectful of cultural heritage. Land use change in our BAU scenario is comparable to socio-economic conditions within the shared socio-economic pathway (SSP) scenario SSP2 ('middle of the road', Popp et al., 2016). Likewise, the scenarios of reduced meat consumption have been uniformly applied across countries. Future scenarios of land-use change associated with alternative diets should encapsulate aspects of fairness and equity (Tilman and Clark, 2014b). For example, a reduction of animal product consumption in developed countries combined with the sustainable trade of meat into countries with animal-protein deficits could simultaneously increase the health of industrialised countries and prevent the destruction of natural land in tropical regions.

Dietary change will be most effective if implemented as part of a suite of demand-side and supply-side measures to reduce biodiversity loss (Tilman et al., 2017; Visconti et al., 2016). In a modelling approach that combined increasing vegetarianism with reduction of food waste, by 2030, agricultural land decreased to a greater extent than we find here under LOW-AP (Wirsenius et al., 2010). Policy screening scenarios similarly found that reaching any biodiversity target will require a combination of strategies: for example, dietary change combined with waste reduction and more efficient agricultural practices (Marchal et al., 2011; Ten Brink et al., 2010). Reducing global meat consumption, and other demand-side measures such as reducing food waste, will be socially and politically complex. It has been suggested that large-scale dietary change will require incentives or regulations (Ripple et al., 2014b). Furthermore, global diet alterations will need to complement food security goals and address global food inequalities. However, biodiversity is an essential component of ecosystem functioning, as well as human well-being, e.g. via provisioning of ecosystem services (IPBES, 2018; Naeem et al., 2016). Furthermore, the conservation of biodiversity and ecosystem services will be essential for maintaining the resilience of the global food system. In developing countries in particular biodiversity can provide a safety net during times of low production and diverse production systems are more resilient to production shocks (Sunderland, 2011). Efforts to preserve biodiversity are, therefore, of the upmost importance and may require dietary change.

Declaration of Competing Interest

The authors declare no competing interests.

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Appendix A. Supplementary data

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