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Title: Winners and losers of national and global efforts to reconcile agricultural intensification and biodiversity conservation

Running head: Intensification and conservation trade-offs

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Abstract

Closing yield gaps within existing croplands, and thereby avoiding further habitat conversions, is a prominently and controversially discussed strategy to meet the rising demand for agricultural products, while minimizing biodiversity impacts. The agricultural intensification associated with such a strategy poses additional threats to biodiversity within agricultural landscapes. The uneven spatial distribution of both yield gaps and biodiversity provides opportunities for reconciling agricultural intensification and biodiversity conservation through spatially optimized intensification. Here, we integrate distribution and habitat information for almost 20,000 vertebrate species with land-cover and land-use datasets. We estimate that projected agricultural intensification between 2000 and 2040 would reduce the global biodiversity value of agricultural lands by 11%, relative to 2000. Contrasting these projections with spatial land-use optimization scenarios reveals that 88% of projected biodiversity loss could be avoided through globally coordinated land-use planning,

implying huge efficiency gains through international cooperation. However, global-scale optimization also implies a highly uneven distribution of costs and benefits, resulting in distinct ‘winners and losers’ in terms of national economic development, food-security, food-sovereignty or conservation. Given conflicting national interests and lacking effective governance mechanisms to guarantee equitable compensation of losers, multi-national land-use optimization seems politically unlikely. In turn, 61% of projected biodiversity loss could be avoided through nationally-focused optimization, and 33% through optimization within just 10 countries. Targeted efforts to improve the capacity for integrated land-use planning for sustainable intensification especially in these countries, including the strengthening of institutions that can arbitrate sub-national land-use conflicts, may offer an effective, yet politically feasible, avenue to better reconcile future trade-offs between agriculture and conservation. The efficiency gains of optimization remained robust when assuming that yields could only be increased to 80% of their potential. Our results highlight the need to better integrate real-world governance, political and economic challenges into sustainable development and global change mitigation research.

Introduction

Closing yield gaps to increase agricultural production on existing croplands could, in theory, curtail future agricultural expansion, a dominant driver of global biodiversity loss (Foley et al., 2005; Pereira, Navarro, & Martins, 2012). Consequently, agricultural intensification has been frequently promoted as an effective strategy to satisfy the increasing demand for agricultural products, while simultaneously minimizing biodiversity impacts (Cunningham et al., 2013). However, land-use intensification itself is a major threat to biodiversity in agricultural landscapes (Benton, Vickery, & Wilson, 2003; Cunningham et al., 2013; Foley et al., 2011; Newbold et al., 2015; Reidsma, Tekelenburg, Van Den Berg, & Alkemade, 2006). High-input agriculture negatively affects multiple taxa and multiple dimensions of biodiversity (Donald, Green, & Heath, 2001; Flynn et al., 2009; Herzon, Auninš, Elts, & Preikša, 2008), in particular farmland species (Benton et al., 2003; Wright, Lake, & Dolman, 2012). These negative effects have mostly been attributed to habitat simplification (Benton et al., 2003), inputs of fertilizer (Kleijn et al., 2009), pesticides (Gibbs, MacKey, & Currie, 2009), and irrigation (De Frutos, Olea, & Mateo-Tomás, 2015; Yamaguchi & Blumwald, 2005).

Past trends and future projections suggest large production increases through intensification on existing croplands (Foley et al., 2011; Van Asselen & Verburg, 2013). Yield increases contributed three quarters of the agricultural production gains between 1985 and 2005 (Foley et al., 2011), and were mainly achieved through enhanced fertilization, irrigation and pest control, shortening of crop rotations and fallow periods, mechanization, and planting of improved crop varieties (Geiger et al., 2010; Loos et al., 2014; Mauser et al., 2015; Tilman, Cassman, Matson, Naylor, & Polasky, 2002). Although yields have stagnated in some parts of the world (Ray, Ramankutty, Mueller, West, & Foley, 2012), large opportunities for increases remain (Mauser et al., 2015; Mueller et al., 2012). Existing land-use projections (Van Asselen & Verburg, 2013) suggest intensification in many parts of the world, including regions of high biodiversity (Orme et al., 2005).

If agricultural lands are to be managed sustainably to ensure biodiversity conservation, while increasing demands are to be met without substantial additional conversion of natural habitats, the least harmful ways of increasing yields need to be identified (Balmford, Green, & Phalan, 2012; Sustainable Development Goals 12 and 15, Aichi Target 7). Various studies have argued that food security could be improved without increasing yields by instead tackling the underlying drivers of demand and inequality (Kehoe et al., 2015; Loos et al., 2014; Tscharntke et al., 2012). However, since real-world motivations for productivity increases also include income generation, agro-economic growth, and energy security, among others, high pressure on agricultural lands remains (Gollin, 2010; Rueda & Lambin, 2014) and production-side measures to reduce biodiversity impacts seem crucial.

While further negative biodiversity impacts through intensification seem inevitable, projected intensification patterns may be suboptimal for minimizing them. To identify possible land-use optimization pathways, production potentials from closing yield gaps need to be contrasted with biodiversity impacts (Balmford et al., 2012). Within a proactive conservation framework, priority would be given to intensification in areas with lowest trade-offs between agricultural intensification and biodiversity conservation, i.e. where highest production gains could be achieved at lowest potential costs to biodiversity, while minimizing further development in areas with high trade-offs. Such land-use optimization could hold great potential for avoiding the most severe biodiversity losses, and may be possible, for instance, via policies enabling integrated land-use planning.

Despite the theoretical appeal of land-use optimization, its real-world implications are poorly understood and largely depend on the spatial scale of such strategies. Nationally-focused optimization strategies may not be the most effective from a global perspective and vice versa (Dobrovolski, Loyola, Da Fonseca, Diniz-Filho, & Araujo, 2014; Pouzols et al., 2014). For instance, production increases in some high-biodiversity countries may be more damaging to global biodiversity than importing food from elsewhere (Phalan, Green, & Balmford, 2014), while unexploited production potential due to national conservation strategies may fuel imports from more biodiverse areas (Lenzen et al., 2012). Global optimization strategies should in principle be able to avoid such inefficiencies, but may interfere with individual countries' interests and needs, for example, related to economic development, food security and sovereignty, or local provision of ecosystem services (Murphy, 2000).

Growth in agricultural productivity is an important driver of economic development, especially in the developing world, where dependence on the agricultural sector is generally high (Gollin, 2010). Countries may be less willing to support global conservation strategies, if these disregard their economic or other strategic interests (Dobrovolski et al., 2014; Hurrell & Kingsbury, 1992). Further socio-economic and political constraints, including competition for land, investment capital, market accessibility, agricultural labor markets, commercial specialization and population pressures may additionally influence the feasibility of optimization strategies (Lambin, Rounsevell, & Geist, 2000; Neumann, Verburg, Stehfest, & Müller, 2010). Such socioeconomic aspects are often neglected in literature on sustainable intensification (Loos et al., 2014). However, understanding the consequences of global strategies for different facets of national development, and investigating alternative pathways, is crucial for assessing their political feasibility.

In this study, we investigated challenges and opportunities for spatially optimized 'sustainable intensification' in the context of national interests, with three distinct aims:

1) to assess the potential decrease in the biodiversity value of existing agricultural lands due to projected intensification patterns,
2) to investigate the potential for averting this biodiversity loss through either nationally-focused or globally coordinated spatial land-use optimization, and
3) to identify potential 'winner' and 'loser' countries of global-scale optimization in terms of national production and conservation opportunities, and to assess relationships between national production opportunities, calorie self-sufficiency and economic dependence on agriculture.

To quantify the biodiversity value of agricultural lands, we estimated the importance of local agricultural lands for the global survival of species, as well as species' likelihoods to persist in these areas amid agricultural intensification. We compared the intensification patterns under the OECD Environmental Outlook (Van Asselen & Verburg, 2013) with two optimization scenarios aimed at reconciling agricultural intensification and biodiversity conservation - one assuming independent optimization by each country and one assuming a globally coordinated strategy.

Materials and methods

The first section of the methods, along with Figure 1, summarizes our analytical approach and the main concepts underlying our models and the results. The subsequent sections provide a more in-depth description of our approach.

Methodological summary

Our approach builds on existing spatially explicit agricultural production estimates and a newly developed metric describing the biodiversity value of agricultural lands. We calculated these two variables for the baseline year 2000 (hereafter referred to as 'current'), when fully closing yield gaps, and for projected intensification patterns, and scaled them to equal-area grid cells of 12,364 km^2 (c. 111-km).

Agricultural production estimates were based on datasets of crop-specific harvested area shares, yield gaps and attainable yields when fully closing yield gaps. For each of the 16 major crops considered, we calculated current production Pc by multiplying harvested area shares HA (fraction of pixel; Monfreda, Ramankutty, & Foley, 2008) with the current yield, i.e. the difference between attainable yields Ya and yield gaps YG (Mueller et al., 2012), and with cell area A (Figs. 1a and 1b).We multiplied harvested area shares with attainable yields and with grid cell area to calculate attainable production Pa (Fig. 1b). To identify current croplands with projected intensification PIp (Fig. 1c), we compared current land-use maps with projections for the year 2040 based on the OECD Environmental Outlook (Van Asselen & Verburg, 2013). We calculated the projected production *Pp* when yield gaps in these areas would be fully closed (note that we neither considered projected expansion nor land abandonment). To compare production among crops, we converted tons to calories using standardized nutritive factors (FAO, 2001).

To calculate biodiversity values of agricultural lands, we combined expert-based extent-of-occurrence range maps for 19,978 species of terrestrial mammals, birds and amphibians (BirdLife International & NatureServe, 2015; IUCN, 2015) with information on their preferred habitat types (BirdLife International, 2015; IUCN, 2015), high-resolution estimates of sub-pixel proportions of different land-cover types (Tuanmu & Jetz, 2014), and an 'agricultural land mask' derived from Ramankutty, Evan, Monfreda, & Foley (2008). Based on the sub-pixel proportions of land-cover, we calculated the preferred habitat area available for each species within the 'agricultural land' pixels (i.e. pixels with any portion of croplands) of each 111-km grid cell and divided this by the total area of available suitable habitat in the species' global distributional range ('global habitat fraction' *H*, Fig. 1d).

In a next step, we estimated the likelihood of a species to persist in cropland and non-cropland proportions of suitable habitats within agricultural lands (*SC* and *SN*, Fig. 1d) at a given intensification level *I* (Fig. 1e), calculated as the fraction of attainable yield achieved (Mueller et al., 2012). To do so, we first used listed habitat preferences to assign each species to one of four habitat categories (forest specialists, natural habitat specialists, marginal cropland users, regular cropland users). Since precise ecological responses to intensification are unknown (Tscharntke et al., 2012), we then defined for each habitat category a distinct space of plausible response functions to increasing agricultural intensification levels, reflecting the species' presumed different sensitivities to agricultural intensification (Fig. 1e).

For each species, we then generated a random response function from within its space of possible responses. These functions were applied to both the cropland and non-cropland proportions of suitable habitat within agricultural lands. However, we accounted for the indirect exposure of non-cropland habitats to intensification on adjacent croplands by additionally weighting in the total cropland proportions *C*. Species' global habitat fractions and likelihoods to persist were then finally weighted by the crop-specific growing area *GA* to optimize intensification for each crop separately (Fig. 1e).

To calculate the crop-specific biodiversity value of agricultural lands *B*, we first integrated the species-level information derived above (global habitat fractions, cropland/non-cropland proportions of suitable habitat within agricultural lands, species' likelihood to persist in suitable habitats within agricultural lands at a given crop-specific intensification level and crop-specific growing areas) and then summed over all species present in a given cell (Fig. 1f). We calculated this biodiversity value for three intensification levels: i) the current fraction of attainable yield achieved *Ic*, ii) the fraction of attainable yield achieved when fully closing yield gaps to the assumed potential, and iii) the fraction of attainable yield needed to achieve projected production gains *Ip* (Fig. 1e).

To assess the potential decrease in the biodiversity value of agricultural lands due to projected intensification patterns (first aim), we compared current and projected biodiversity values summed over all crops (Fig. 1i). To investigate the potential for averting the projected biodiversity loss through spatial optimization (second aim), we first quantified crop-specific trade-offs between agricultural intensification on existing croplands and biodiversity conservation (intensification-biodiversity trade-offs, Fig. 1g). To this end, we divided the decrease in the crop-specific biodiversity value when fully closing yield gaps (i.e. the biodiversity loss ΔB) by the associated production gain (i.e. the production gap ΔP, analogous to yield gaps). We then developed two scenarios for achieving projected production volumes by prioritizing areas with the lowest intensification-biodiversity trade-offs for intensification (priority sequence, Fig. 1h), one optimizing at the national and one at the global level (Fig. 1i). While the national scenario aimed to achieve the projected country-specific production gains, the global scenario only achieved projected gains on the global level. For both scenarios, we compared the respective biodiversity values to the projected one. To identify potential 'winner' and 'loser' countries, we contrasted country-specific developments of total production and biodiversity values in either scenario with each country's national calorie self-sufficiency and national economic reliance on agriculture, (aim 3). Because economic and management factors may limit the potential to fully close yield gaps, we performed a sensitivity analysis based on the assumption that maximally 80% of the attainable yields can be achieved.

To account for uncertainties in our estimates of biodiversity values, we repeated both approaches (full and partial closing of yield gaps) 1000 times. In each run, we generated a new random species-specific response function to agricultural intensification and randomly added or removed up to 50% of the original global habitat fractions. The methodological approach, datasets and reasoning are described in detail below, and summarized in Fig. 1. Details on the datasets used are given in Table S1, and the most important methodological and conceptual terms are defined in Table 1.

Input land-use layers

We used data on current harvested area shares *HA* (fraction of pixel; Monfreda et al., 2008), and on attainable yields *Ya* and yield gaps *YG* (difference between attainable yields when fully closing yield gaps and current yields; Mueller et al., 2012) for 16 major crops to calculate spatially explicit agricultural production (Fig. 1a, Table S4 for the investigated crops). We aggregated these datasets from their original resolution (5 arc-min) to the c. 111-km resolution of the equal-area grid (taking pixel means). The selected crops cover more than 50% of the world's croplands and provide more than 80% of the global crop calories (West et al., 2014). To compare production among crops, we converted yield measures from tons to calories using standardized nutritive factors (FAO, 2001).

Current and potential crop production

For each crop, we multiplied the aggregated harvested area shares with the current yield, i.e. the difference between attainable yields and yield gaps, and with the 111-km grid cell area to calculate current production *Pc* (Fig. 1b). Likewise, we multiplied the harvested area shares with attainable yields and grid cell area to calculate attainable production *Pa*. We used the difference between attainable and current production, i.e. the production gap ΔP, to quantify crop-specific intensification-biodiversity trade-offs (see section *National scenario* below).

Projected crop production in 2040

We extracted projected intensification patterns from the global land change model CLUMondo, using modeled areas of future intensification (year 2040) under the OECD Environmental Outlook (Van Asselen & Verburg, 2013; note that we did not consider projected expansion, as our study was focused on existing croplands). We compared the land-use maps for 2000 and 2040 (5 arc-min resolution) to identify pixels with projected intensification by 2040 *PIp*, from which we created a binary map (1 = projected intensification, 0 = no intensification, Fig. 1c). We multiplied this map with the harvested area shares of each crop to calculate the harvested area shares with projected intensification by 2040 *HApi*, which we aggregated to the 111-km grid cells of the equal-area grid (taking pixel means). We then multiplied *HApi* with the yield gap and with the 111-km grid cell area, and added the current production to obtain projected production *Pp*. Accordingly, we assumed that yield gaps will be fully closed in all croplands projected to undergo some intensification , because the land systems of Van Asselen & Verburg (2013) were not directly transferrable to the yield estimates of the agricultural production data used here. Thus, we potentially overestimated production and the intensification-related decrease in the biodiversity value under the projections. For the same reason and because we only considered existing croplands, we ignored extensification and abandonment, which is projected for some cropland systems (Van Asselen & Verburg, 2013).

Species distribution information

We used global expert-based extent-of-occurrence range maps for 19,978 species of terrestrial mammals, birds and amphibians (BirdLife International & NatureServe, 2015; IUCN, 2015; Fig. 1d). Although these three vertebrate groups represent only a small fraction of biodiversity (Costello, May, & Stork, 2013), they do represent taxa of particularly high *de facto* conservation relevance, and they are the only large taxonomic groups where comprehensive global information on distributions and habitat preferences is available for almost all species. We scaled the range maps to an equal-area grid of 12,364 km^2 cell size (c. 111 x 111 km at the equator), to reduce the severe overestimation of species' areas of occupancy at finer spatial grains (Hurlbert & Jetz, 2007).

Global habitat fractions within agricultural lands

We used 1-km resolution estimates of sub-pixel proportions of different land-cover types (Tuanmu & Jetz, 2014) to identify 'agricultural land' pixels, i.e. those pixels with any portion of croplands (Fig. 1d). To increase consistency with our other land-use datasets, we only considered those agricultural land pixels falling within our 'agricultural land mask', i.e. within the 5 arc-min pixels that according to Ramankutty et al. (2008) contain croplands. In a next step, we defined the 'suitable habitat' for each species, i.e. the specific areas where the species could plausibly occur, based on the availability of land-cover types that correspond to that species' preferred habitat types (BirdLife International, 2015; IUCN, 2015; Table S2), similar to Rondinini, Stuart, & Boitani (2005). For each species and grid cell, we then calculated 'global habitat fraction' H (Fig. 1d), i.e. the fraction of the range-wide suitable habitat that is contained within the agricultural lands of the focal grid cell. To do so, we first calculated the global area of each species' suitable habitat, by summing the sub-pixel portions of suitable land-cover types across all 1-km pixels falling within the range-intersecting 111-km grid cells. We then summed the portions of suitable habitat types falling only within the 1-km 'agricultural land' pixels of each 111-km grid cell and divided these sums by the species' global area of suitable habitat. We calculated global habitat fractions as weighted metrics: land-cover classes corresponding to habitat types indicated as 'suitable' were fully-weighted, whereas land-cover classes corresponding to habitat types listed as 'marginal' or 'unknown' were weighted by 50% (e.g. if marginal habitat covers 10% of a 1-km pixel, it would be counted as 5%). A global habitat fraction equaling 1 means that all suitable habitat within a species' global range is entirely contained within the agricultural land pixels of the focal grid cell. Thus, this metric can be interpreted as the importance of the local agricultural lands for the global survival of a species, and is typically highest for range-restricted species occurring in human-dominated landscapes. The sum of habitat fractions across all species in an area can thus be interpreted as the importance of this area's agricultural lands for global biodiversity. We note that this measure does not account for potential effects of habitat fragmentation *per se* on species persistence (i.e. beyond the implied habitat loss; Fahrig, 2003). While we partly compensated for the coarse nature of range map data by considering fine-resolution habitat availability, the quality of the used information on species' habitat preferences is biased towards better known species (Peterson, Navarro-Sigüenza, & Gordillo, 2016), and species' fine-scale occurrences within different parts of their ranges, even within suitable habitats, are often highly uncertain (Meyer, Jetz, Guralnick, Fritz, & Kreft, 2016). To account for both sources of uncertainty, we randomly added or removed up to 50% of the original global habitat fractions for each grid cell in each of the 1000 analysis runs.

Cropland/non-cropland proportions of suitable habitat within agricultural lands

For each species within the agricultural lands of each 111-km grid cell, we distinguished between the cropland (*SC*) and non-cropland proportions of suitable habitat (*SN*), in order to account for different impacts of intensification (Fig.1d, see section *Crop-specific intensification level* below). For instance, if the agricultural land pixels of a grid cell were 60% covered with forest, 30% with savanna and 10% with cropland, an open-habitat species that regularly uses both cropland and savanna had an *SC* of 0.25 and an *SN* of 0.75.

Crop-specific intensification level

Apart from the immediate impact of intensification on existing croplands, surrounding non-cropland areas can also be negatively affected, e.g. through fertilizer and pesticide run-off (Matson & Vitousek, 2006; Tilman et al., 2002). We assumed that the exposure to intensification is greater for cropland than for non-cropland proportions of suitable habitat within agricultural lands. To estimate the crop-specific intensification level to which the cropland proportions of suitable habitat are exposed, we calculated the crop-specific fraction of attainable yield achieved *I* (Fig. 1e), which is typically controlled by levels of fertilizer input and irrigation (Mueller et al., 2012). For the non-cropland proportions of suitable habitat, we additionally multiplied this fraction with the total cropland proportions *C* of agricultural lands pixels inside a grid cell, such that non-cropland proportions of suitable habitat surrounded by more croplands would have a higher exposure to a given intensification level. To calculate the current intensification level *Ic*, we divided the current yield, i.e. the difference between attainable yields and yield gaps, by the attainable yields (Mueller et al., 2012). When fully closing yield gaps, this fraction is 1 (i.e. full intensification). We approximated the projected intensification level in 2040, *Ip*, by dividing current crop production by the projected crop production in 2040 (see section *Projected crop production in 2040* above). We note that while biodiversity loss is not a direct function of yield increases *per se*, we here use the closing of yield gaps as a proxy for the typically associated management practices (e.g. increased agrochemical inputs).

Species' likelihood to persist in suitable habitats within agricultural lands at a given crop-specific intensification level

Species differ greatly in their sensitivities to agricultural intensification. However, detailed information on species' responses to agricultural intensification does not exist for the majority of species, although substantial advances in compiling such information have recently been made (Hudson et al., 2014). Nevertheless, case studies and ecological theory allow for certain expectations of how different types of species may respond. For instance, available evidence points to strict forest specialists (i.e. species that are never observed outside of forests) being particularly sensitive to any kind of habitat opening or altered forest structure (Gibson et al., 2011). These species can be expected to be mostly absent from even the most extensively used agricultural lands, e.g. where small and extensively managed agricultural fields with frequent and long fallow periods are interspersed with natural habitat patches, which would correspond to the very lowest section on our intensification scale (Fig. 1e, green lines). In contrast, natural habitat specialists that better cope with more open habitats, may still thrive in such areas due to greater structural similarities with their natural habitats, but these species will become much rarer when agricultural lands become slightly higher-yielding, such as in most European ‘extensive’ agricultural landscapes (i.e. less frequent and shorter fallow periods, increasingly larger field sizes, use of heavy machinery; Fig. 1e, brown lines). Species more adapted to croplands may still thrive in such landscapes, but will be severely affected once intensification levels become even higher (Fig. 1e, yellow and red lines; Wright et al., 2012). Accordingly, in an exemplary intensively managed agricultural landscape in Europe, forest specialists would already have reached very low likelihoods to persist a long time ago, hence further intensification would only have relatively limited additional impact. In contrast, natural habitat specialists and species using croplands may still be more likely to persist under recent conditions, but further intensification will lead to comparably much steeper drops in their persistence likelihoods.

To parameterize our model of biodiversity responses to intensification for such different species types, we first used data on habitat preferences (BirdLife International, 2015; IUCN, 2015), and classified all species into four major *habitat categories*, for which we assumed distinct sensitivities to agricultural intensification (from most to least sensitive): i) forest specialists (7,438 species reported as only living in forest), ii) natural habitat specialists (4,727 species only living in non-artificial habitats, including in open habitats), iii) marginal cropland users (1,092 species), and vi) regular cropland users (6,721 species; see Table S2 for details). For each habitat category, we then defined a very broad space that encompassed a wide range of possible trajectories for a species' persistence in suitable habitats within agricultural lands under increasing intensification levels (Fig. 1e and Table S3; compare Seppelt et al., 2016). For each species, we then generated a random response function from within its space of possible responses during each of the 1000 analysis runs. We acknowledge that the possibility of crop-specific species responses may introduce further uncertainties to our results (Donald, 2004).

Crop-specific growing areas

To optimize intensification for each crop separately, we additionally weighted in the crop-specific growing area shares *GA* (Fig. 1e), which we calculated by summing maximum rain-fed and irrigated growing areas for each crop (Portmann, Siebert, & Döll, 2010) and dividing this sum by the total cropland proportions of agricultural lands multiplied by the pixel area (Ramankutty et al., 2008). Where the combined growing area shares of all 16 crops exceeded the reported total cropland proportions due to data inconsistencies, we used the proportion of the combined area of all crops instead. We then aggregated these datasets (5 arc-min original resolution) to the 111-km resolution of the equal-area grid (taking pixel means). Note that the addition of crop-specific values to obtain the total biodiversity value may introduce bias when multiple crops are grown on the same field (e.g. in multi-crop rotation systems). Additionally, we note that suitable habitat may not be equally distributed among fields with different crops, thus multiplying global habitat fractions within agricultural lands by average growing area shares within grid cells may blur crop-specific differences in biodiversity impacts. However, aggregating growing areas to the grid cell level is reasonable given that data quality on the original resolution (5-arc min) is limited (Monfreda et al., 2008).

Biodiversity value of agricultural lands

We combined global habitat fractions within agricultural lands, cropland/non-cropland proportions of suitable habitat within agricultural lands, species' likelihood to persist in suitable habitats within agricultural lands at a given crop-specific intensification level and crop-specific growing areas to calculate the global biodiversity value of agricultural lands. We first calculated the biodiversity value separately for each species and crop, and then summed up these values across all species to obtain the *crop-specific* biodiversity value of the agricultural lands of a given grid cell (equation 1, Fig. 1f). We calculated the biodiversity value for three intensification levels; those for the year 2000, those when fully closing yield gaps and those projected. We used the difference between the current crop-specific biodiversity value and that when fully closing yield gaps (i.e. the biodiversity loss ΔB, Fig. 1f) to quantify crop-specific intensification-biodiversity trade-offs (see section *National scenario* below). The crop-specific biodiversity value of agricultural lands at a given intensification level is calculated as:

$$B_{c,a,k} = \sum_{s=1}^{n} H_{s,c,k} \times [SC_{s,c} \times fun_{s,k}(I_{a,c}) + SN_{s,c} \times fun_{s,k}(I_{a,c} \times C_c)] \times GA_{a,c} \text{ (equation 1)}$$

where $B_{c,a,k}$ is the biodiversity value of crop a in the agricultural lands of cell c in run k, $H_{s,c,k}$ is the global habitat fraction of species s within the agricultural lands in cell c (randomly varied up to 50% in each run k), i.e. the local suitable habitat within local agricultural lands as a fraction of the total suitable habitat area within that species' global range, $SC_{s,c}$ and $SN_{s,c}$ are the cropland and non-cropland proportions of suitable habitat for species s within the agricultural lands of cell c ($SC_{s,c} + SN_{s,c} = 1$), $fun_{s,k}()$ is the response function estimating species s' likelihood to persist in suitable habitats within agricultural lands at a given crop-specific intensification level, which is randomly drawn for the k'th time from the assumed space of species s' possible response to agricultural intensification, $I_{a,c}$ is the crop-specific intensification level of crop a in cell c, C_c is the total cropland proportion of the agricultural lands in cell c, and $GA_{a,c}$ is the growing area share of crop a in cell c as a proportion of C_c.

Land-use optimization scenarios

National scenario. In the national scenario, countries aim to achieve projected national production volumes from agricultural intensification with lowest possible national biodiversity impacts. The biodiversity value is calculated according to global habitat fractions (equation 1), i.e. we assumed that countries account for the global importance of the species inhabiting their country (e.g. analogous to species currently defined as of 'international importance' on several countries' national red lists). We note that the importance of agricultural lands could also be evaluated on the national scale or by using different prioritization approaches. We first calculated cell- and crop-specific trade-offs to define each countries' crop-specific optimization sequence (i.e. from lowest to highest trade-offs, Figs. 1g and 1h). To quantify these trade-offs, we divided the decrease in the biodiversity value when fully closing the yield gap of a crop (biodiversity loss) by the associated production gain (production gap), i.e. the costs to biodiversity that result from a certain production gain. For each crop, each country would then independently prioritize (i.e. intensify) the cells with the lowest national trade-offs, until its projected crop-specific production volume from intensification was achieved. Accordingly, we calculated the biodiversity values and production gains when fully closing yield gaps for all prioritized cells except for the last one (for which only partial intensification was required to meet the projected national production value for each crop), while calculating current biodiversity and production values for the remaining cells. To additionally explore optimization potential beyond the projected production volumes, we continued intensification along the prioritization sequence until all yield gaps were fully closed. At each intensification level we summed the biodiversity values and production across all crops to obtain the *overall* biodiversity and production values.

Global scenario. In the global scenario, we assumed international coordination to achieve projected global production volumes for each crop from agricultural intensification, where this would incur the lowest possible biodiversity impacts globally. Trade-offs, biodiversity values and production gains were calculated according to the national scenario. The only difference to the national scenario is that the crop-specific prioritization sequence started with the cells with the lowest *global* trade-offs, and continued along the global sequence until the projected production volume was achieved. Therefore, this scenario ignores projected country-specific production gains.

Socio-economic and ecological implications in the global scenario. For any one country, optimization under the national scenario will not affect national agricultural production, but possibly reduce biodiversity impacts relative to projections. Optimization under the global scenario, however, may negatively affect country-specific socio-economic and ecological parameters in multiple ways. To assess the political feasibility of globally coordinated land-use optimization, we identified 'winner' and 'loser' countries under the global scenario, by comparing overall production gains and retained biodiversity values under the two scenarios. To further assess implications of global optimization for national food security, food sovereignty, and development opportunities, we calculated the Gini coefficients of inequality in future production increase (Zeileis, 2014), as well as pairwise Spearman's rank correlations between the difference of national production gains under the two scenarios and i) national calorie self-sufficiency (agricultural production volumes divided by the calorie demand estimates of Pradhan, Fischer, van Velthuizen, Reusser, and Kropp (2015), summed to the country level) and ii) the national economic reliance on agriculture (approximated by the percentage of GDP added by agriculture, forestry and fishing; FAOSTAT, 2015). Finally, we calculated the total production deficit of the 'loser' countries in the global scenario (overall country-specific projected production gains minus production gains achieved in the global scenario summed across all ‘loser’ countries), i.e. the production volume which would need to be exchanged from production ‘winners’ to ‘losers’ to balance production losses.

Partial closing of yield gaps

Several economic and management factors may limit the potential to fully close yield gaps. It has been found that yields typically plateau when they reach 75 – 85% of their potential (Lobell, Cassman, & Field, 2009; Van Wart, Kersebaum, Peng, Milner, & Cassman, 2013). We therefore repeated all our analyses with the assumption that yields can maximally achieve 80% of their potential. Where current yields were already higher, we kept the values constant (i.e. no additional production and identical biodiversity value).

Outputs

We drew our main conclusions from relative changes of overall production and biodiversity value summed across the national and global level, compared to the current conditions, as well as from avoided biodiversity losses, i.e. the portion of the projected biodiversity impacts which can be avoided through optimization (difference between optimized and projected biodiversity value on the national or global level divided by the globally projected biodiversity loss). To contrast the national and global scenario, we calculated the ratios of overall production and biodiversity changes on the national level (i.e. changes under the global scenario divided by the changes under the national scenario).

From the scenario analyses, where we assumed only partial closing of yield gaps, we extracted the results that were most relevant for our main conclusions and compared them with the results from the main analysis (full closing of yield gaps). Additionally, we calculated pairwise Spearman's rank correlations of the relevant country- and crop-specific biodiversity and production values between the main analysis and when only partially closing yield gaps.

All analyses and calculations were performed using R 3.2.2 (R Core Team, 2016), running in a high-performance computing environment (Intel E5-2640 v3, 20 cores, 64 GB RAM).

Results

Projections and scenarios

Projected agricultural intensification led to an estimated 11.1% decrease in the global biodiversity value of agricultural lands (range = 10.7–11.4%), compared to current conditions, while leading to a global production gain of 20.3% (Fig. 2). When assuming that yields would be maximally increased to 80% of their potential (yielding a global production gain of only 12.2%, hereafter abbreviated as ‘Y-80’), the global biodiversity value would decrease by 6.0% (range = 5.8–6.2%). The national optimization scenario in turn led to a decrease in biodiversity value of 4.3% (range = 4.1–4.7%; or 2.4%, range = 2.3–2.6% for Y-80) when achieving the projected production increase (Fig. 2). In other words, 60.9% (range = 58.3–61.6%) of the projected biodiversity loss was avoided under this scenario (59.8%, range = 57.9–60.5% for Y-80). Ten countries alone were responsible for reducing the projected biodiversity loss by 32.9% (Table 2), while these countries would still achieve their projected production gains. When increasing yields to 80%, a nearly identical set of countries (Tanzania would replace Vietnam) would reduce the projected biodiversity loss by 32.4%. Moreover, 96 countries could reduce their projected domestic biodiversity impacts from future intensification by more than 50% each (Table S5; 81 countries for Y-80).

The global optimization scenario achieved the projected production gain from intensification with only a modest decrease in the current global biodiversity value (1.4%, range = 1.3–1.5%; 0.7%, range = 0.7–0.8% for Y-80, Fig. 2). Accordingly, 87.7% (range = 86.7–87.8%) of the projected biodiversity loss was avoided (88.3%, range = 87.5–88.4% for Y-80). This was mainly due to a prioritization of intensification in low-biodiversity areas with prevalent production gaps, mainly in the northern hemisphere (Fig. 3), with 67.2% (range = 66.0–68.3%; 68.1%, range = 67.1–69.4 for Y-80) of all intensified cells lying outside of the tropics, compared to 56.7% (range = 55.6–57.8%; 56.2%, range = 54.9–57.4 for Y-80) in the national scenario. The proportion of cells prioritized for intensification were similar under the global and national scenario (52.9%, range = 51.2–54.4% vs. 50.9%, range = 49.7–52.0%; 51.3%, range = 49.9–52.6% vs. 49.3%, range = 48.2–50.5% for Y-80), but only reached about three quarters of the proportion under the projections (70.4%; 69.4% for Y-80).

In the national scenario, maintaining biodiversity values of more than 90% of the current value was possible for all crops except for rye (Table S4; more than 94% for Y-80). In the global scenario, the retained biodiversity values of all crops except rye even exceeded 95% (97% for Y-80) and reached up to 99.5% for potato (range = 99.4–99.5%; 99.7% for Y-80), suggesting large potentials for impact reduction. Full intensification of all existing croplands led to a 37.3% decline of the global biodiversity value (range = 36.8–37.7%, Fig. S1; 19.0%, range = 18.7–19.3% for Y-80), but decreases varied between 17.5% and 59.4% for crops (Table S4), and between 0.03% and 98.5% for countries (Table S5). The respective country- and crop-specific decreases when increasing yields to 80% were highly correlated (Spearman's rho = 0.9, $p < 0.05$).

Socio-economic and ecological consequences in the global scenario

The socio-economic and ecological consequences in the global scenario varied widely between countries. Production gains in the global scenario were unequally distributed (Gini coefficient = 0.8; same value for Y-80), especially favoring northern over southern-hemisphere countries (Fig. 4a). In total, 25 countries more than quadrupled their projected production gains, of which 20 are listed as high- or upper-middle-income economies, whereas 47 countries achieved less than one quarter of their projected gains, of which 28 are considered as low- or lower-middle-income countries (Table S5; World Bank, 2016). Country-specific production gains were highly correlated with those when assuming that yields can only be increased to 80% (Spearman's *rho* = 0.97, $p < 0.05$). To balance production losses in the global scenario, more than one third of all production gains would need to be traded from production 'winners' to production 'losers' (same value for Y-80). Production gains in the global scenario were positively correlated with calorie self-sufficiency (Spearman's *rho* = 0.3, $p < 0.05$; same for Y-80), i.e. the countries where more food is most urgently needed would generally achieve lower production gains than projected. In the global scenario, production gains were negatively correlated with the national economic reliance on agriculture (Spearman's *rho* = -0.3, $p < 0.05$; same for Y-80), i.e. countries that are economically more dependent on agriculture achieved lower production gains. The production 'winners' in the global scenario experienced decreases in the biodiversity value down to around half of the current value (Fig. 4b and Table S5). The respective country-specific decreases were again highly correlated to those when assuming that yield gaps can only be increased to 80% (Spearman's *rho* = 0.9, $p < 0.05$).

Seven countries may be considered as both production and biodiversity 'winners' in the global scenario (highest two quartiles regarding production gain and biodiversity value; six countries for Y-80), while eight countries lost regarding both dimensions (Fig. 4c-e; seven countries for Y-80). The remaining countries in our analysis were 'winners' in either production (72 countries; 73 for Y-80) or biodiversity (69 countries; 70 for Y-80), but not both.

Discussion

Based on our calculations, the global biodiversity value of existing agricultural lands will decrease by c. 11% by 2040 if agricultural intensification continues as currently predicted. This decline is mainly due to large-scale intensification in high-biodiversity regions, namely in Africa, Argentina, Australia, Brazil, China, India and Mexico, of which most have been previously identified as areas of high conflict between conservation and future intensification (Shackelford, Steward, German, Sait, & Benton, 2015). However, considerable intensification is also projected in less biodiverse areas such as in Eastern Europe, Northern America and Russia. Overall, our results demonstrate that despite the severe biodiversity loss incurred from agricultural expansion and intensification to date (Foley et al., 2005; Newbold et al., 2015), relatively high production gains could still be achieved without a considerable additional decline of the global biodiversity value of present-day agricultural lands. This is mainly because high biodiversity values are largely concentrated in agricultural lands where relatively small croplands are surrounded by extensive natural habitats, and where the negative impacts of intensification would thus be limited (Spearman's $rho = 0.5$, $p < 0.05$, for the correlation between global habitat fractions and the non-cropland proportions of agricultural land pixels). Nevertheless, full intensification on all existing croplands would lead to a 37% decrease in the global biodiversity value of agricultural lands (Fig. S1).

Our scenario analyses revealed that the projected biodiversity loss could be reduced by about 61% or 88%, respectively, through nationally-focused or globally coordinated spatial land-use optimization. This means that any policies leveraging integrated land-use planning over broad spatial scales have the potential to lead to tremendous efficiency gains. These efficiency gains remained robust when assuming that yields could only be increased to 80% of their potential, although the overall lower intensification levels would naturally imply substantially lower production gains as well as lower absolute biodiversity losses.

About one third of the projected biodiversity loss could already be avoided by enabling land-use optimization in only ten countries. Four of these 'leverage countries' (Brazil, China, India and Indonesia) have previously been identified as leverage points for the reduction of other key environmental impacts of agriculture such as N_2O emissions, and water and fertilizer consumption (West et al., 2014). Most of the ten countries, however, are among the 20 worst-ranked countries in terms of relative and/or absolute environmental impacts (Bradshaw, Giam, & Sodhi, 2010). Furthermore, many of these countries are characterized by strong subnational socio-economic differences, heterogeneous political interest groups, and relatively weak land-governance institutions, which currently impede country-wide land-use optimization. Improving these countries' capacities for broad-scale, integrated land-use planning may thus be particularly helpful for realizing the efficiency gains identified in this study. This may include, for instance, fostering the institutionalization of spatial planning in land-development processes, training of government staff in multi-criteria optimization techniques, improving access to free, high-quality datasets on land use and biodiversity (Weeks et al., 2014), and strengthening institutions that can arbitrate subnational land-use conflicts (Rudel & Meyfroidt, 2014).

Even greater reductions of projected biodiversity loss could be achieved via globally optimized land-use intensification. This finding adds further weight to recent discussions on the environmental gains that could be achieved through better international coordination and cooperation (Dobrovolski et al., 2014; Meyer, Kreft, Guralnick, & Jetz, 2015; Pouzols et al., 2014). Yield gaps in the global optimization scenario would be primarily closed in the temperate Northern Hemisphere, where biodiversity values of agricultural lands are generally lower. In turn, biodiversity-rich countries such as Nicaragua or the Philippines would largely retain their high biodiversity values. This global scenario, however, would also imply drastic socio-economic consequences for several countries. For instance, we found that less calorie self-sufficient countries would achieve comparatively lower production gains relative to the national scenario, and that many countries requiring high increases to meet their demand would be entirely neglected. Further, countries that are economically more dependent on agriculture would experience more severe trade-offs when participating in a global optimization strategy.

On a proportional scale, the global scenario implies considerable biodiversity loss in the 'production winner' countries. For instance, intensification in some European countries would reduce the current biodiversity values of agricultural lands by about one sixth (e.g. Romania), one quarter (e.g. Lithuania) or even one half (Denmark). Potential negative effects of biodiversity loss on ecosystem functioning, ecosystem services, resilience, socio-cultural values and ultimately human wellbeing in agricultural areas of these regions require careful attention (Cardinale et al., 2012; Loos et al., 2014; Tscharntke et al., 2012). Accordingly, this scenario contradicts current nationally-focused efforts to meet international conservation commitments and obligations, such as the United Nations Aichi targets, or the agri-environmental schemes of the European Union.

Our scenario comparison can offer quantitative insights into the potential national motivations of individual countries when negotiating international sustainable development strategies (Farell, 2017). Global players such as Canada, China, France, Germany, the United Kingdom or the United States might be supporters of a global optimization strategy from an agro-economic perspective. In turn, opposition might be expected especially from highly-biodiverse, low- and lower-middle-income countries due to their substantially compromised production and development opportunities (Fig. 4). Several countries, such as Botswana, Colombia and Lao PDR, would achieve much higher production gains if optimization only happened at the national scale, without significantly higher biodiversity loss compared to the global scenario. Without international governance mechanisms and effective compensation of such ‘losers’ of global optimization, for instance, through a fair distribution of production surpluses or monetary compensation of the opportunity costs of conservation, any global-scale land-use optimization seems politically unfeasible (Hurrell & Kingsbury, 1992; James, Gaston, & Balmford, 1999).

Our results also demonstrate that the national implications of land-use optimization at either spatial scale would change substantially with increasing global production levels. For instance, while global-scale optimization would immediately be highly advantageous for production in the United States, the bulk of Nicaragua’s conservation benefits relative to the national scenario would only materialize much later (Fig. 4 d-e). Further research evaluating such shifting intensification-biodiversity trade-offs against planned or projected development trajectories of individual countries could provide additional insights regarding feasible intensification strategies, and may also help inform conservation actors about the optimal timing of interventions (Radeloff et al., 2013). As sustainable intensification strategies that rely on effective global land governance (Creutzig, 2017) may be unrealistic amid conflicting national interests, future studies should further explore national- or even subnational-scale options, especially in regions of high biodiversity-intensification trade-offs. As land-use interests may diverge as strongly within as between countries, understanding subnational winners and losers will be crucial for assessing regional development opportunities and the political feasibility of integrated land-use planning.

Future agricultural demand is expected to increase by 59-98% by 2050 compared to the year 2005 (Valin et al., 2014). However, the yield datasets underlying our analyses suggest a production gain of only c. 60%, even if yield gaps were closed globally (Mueller et al., 2012), of which only c. one third would be realized by 2040 according to projections. If most of the future production gains are to be achieved mainly on existing croplands, opportunities for spatial optimization of intensification would thus be hindered, and largely diminish beyond a global production gain of c. 50% (Fig. S1, c. 30% when yields would be maximally increased to 80% of their potential). However, a recent study suggests that production gains through improved crop management and more efficient allocation of crops may be higher than the estimates used here and could even exceed future demand (Mauser et al., 2015), thus leaving room for spatial optimization, such as in this study.

Our approach to estimating intensification-driven biodiversity loss addresses multiple sources of uncertainty. As expected, random changes of species-specific response-functions and random perturbations of global habitat fractions, as implemented in this study, translated into high uncertainties in the absolute losses of biodiversity (Tables S4 and S5), as well as in prioritization results at the level of individual grid cells (Fig. S2). However, these uncertainties decreased drastically when evaluating relative losses aggregated over national (Table S5) or global extents (Figs. 2 and S1), and thus do not affect the main conclusions of this study. Highly pronounced global patterns of habitat fractions and yield gaps are the main reasons for this robustness of our results. However, uncertainties in available information on yields, yield gaps, and especially in future land-use remain unresolved issues (Monfreda et al., 2008; Prestele et al., 2016). Furthermore, our approach ignores possible indirect effects of intensification on biodiversity beyond agricultural lands, e.g. due to associated habitat fragmentation, agrochemical run-offs, or changes in biogeochemical cycles (Benton et al., 2003; Foley et al., 2005; Matson & Vitousek, 2006; Tilman et al., 2002).

Despite these caveats, our results clearly demonstrate the potential biodiversity benefits of carefully planned land-use intensification strategies compared to projected intensification patterns. We should stress, however, that any real-world implementation of such strategies would be hampered by a variety of socio-economic and political factors. Furthermore, due to rebound effects through increased economic profitability of agriculture or lower food prices boosting consumption, higher yields are no guarantee for more land being spared for nature

(Lambin & Meyfroidt, 2011; Perfecto & Vandermeer, 2010; Tscharntke et al., 2012; Villoria, Byerlee, & Stevenson, 2014), unless intensification can be effectively coupled with habitat protection (Phalan et al., 2016). Moreover, where short-term yield increases are achieved via inappropriate management, resulting land degradation might even lead to local productivity losses, further boosting cropland expansion elsewhere (Lambin & Meyfroidt, 2011).

This study was designed to investigate the potential avoidance of biodiversity loss through spatially optimized intensification on existing croplands, i.e. via a land sparing approach. In reality, future increases in agricultural production will most likely be achieved by a combination of intensification and expansion, while productivity increases in some places may also drive land abandonment elsewhere (Queiroz, Beilin, Folke, & Lindborg, 2014). Hence, an important question for future research is how agriculture-biodiversity trade-offs may be reconciled via policies fostering optimal regional mixes of these processes. Further research could evaluate in how far globally differing potentials for agrotechnological innovation and diffusion may affect the degree to which regional yield gaps can be closed and land-use be optimized. Moreover, further studies could systematically compare production trade-offs for alternative conservation strategies, e.g. accounting for evolutionary distinctiveness or species' importance for ecosystem functioning (Pollock, Thuiller, & Jetz, 2017), national stewardship of species (Schmeller et al., 2008), or existing agendas of international conservation actors (Eken et al., 2004). Currently, uncertain species' responses to agricultural intensification are the biggest weakness of our model. Consequently, when more comprehensive datasets on species-specific responses to agricultural land-use become available (e.g. through the PREDICTS initiative; Hudson et al., 2014), and the quality of the underlying datasets increases, our assessment needs to be updated to provide a more comprehensive evaluation of the biodiversity value of agricultural lands.

In conclusion, we found that most projected biodiversity loss from agricultural intensification could be avoided by intensifying land-use in a spatially optimized manner. These conclusions are robust to alternative assumptions on possible yield increases. Further, we found that spatial scale mediates the compatibility between optimization strategies and countries' national interests. Our identification of 'winner' and 'loser' countries may provide a valuable baseline for discussions about fair and equitable international conservation and land-use optimization strategies. These results may also guide international donors and capacity-building institutions in making strategic investments. Effective 'sustainable intensification' faces various real-world constraints, especially when relying on international cooperation. Hence, we argue that a feasible yet effective way of reducing the global footprint of agriculture on biodiversity could be the targeted capacity-building for integrated land-use planning at national scales, particularly in a few identified 'leverage' countries where the potential for reconciling intensification-biodiversity trade-offs would be greatest.

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Author contributions

LE, CM, TT and CS designed the study. LE and CM developed the methods, collected the datasets, performed the analyses, and designed the figures. All authors discussed and interpreted the results. LE and CM wrote the manuscript. All authors contributed substantially to revisions.

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Tables

Table 1. Definition of the most important methodological and conceptual terms used in the present study.

Term	Definition in the context of this study
Agricultural intensification	Closing yield gaps, i.e. increasing the crop-specific intensification level on existing croplands.
Agricultural lands	Pixels with any portion of croplands (i.e. ignoring pasturelands).
Croplands	The areas where the crops are actually grown.
Intensification-biodiversity trade-off	The decrease in the crop-specific biodiversity value when fully closing yield gaps (biodiversity loss), divided by the associated production gain (production gap).
Land-use optimization	Targeted efforts to prioritize the cells with the lowest intensification-biodiversity trade-offs for agricultural intensification on existing croplands.
Projected production	Production which would be achieved if yield gaps were fully closed in all cells in which intensification on existing croplands is projected by 2040 under the OECD Environmental Outlook (i.e. explicitly excluding any projected expansion).

Table 2. Top-ten countries with the highest potential to reduce projected global biodiversity loss incurred by achieving projected production gains via agricultural intensification in the national scenario. The projections are based on the OECD Environmental Outlook. The national scenario assumes that each country independently prioritizes the cells with the lowest national intensification-biodiversity trade-offs for intensification, until that country's projected production volume is achieved. Column 2 indicates production gains achieved for the projections, and under a national land-use optimization scenario, relative to the baseline year 2000. Columns 3-4 indicate the biodiversity value retained in agricultural lands under the projections and the national scenario relative to the baseline value. Column 5 shows the estimated relative avoidance of the projected global biodiversity loss under the national optimization scenario (difference between optimized and projected biodiversity value on the national level divided by the globally projected biodiversity loss). Values in brackets indicate the range of the predictions over 1000 model runs.

Country	Production gain under the projections / national scenario (%)*	Retained biodiversity value under the projections (%)	Retained biodiversity value under the national scenario (%)	Projected global biodiversity loss avoided under the national scenario (%)
India	32.6	71.9 (70.1- 73.9)	84.4 (82.7- 85.9)	5.8 (5.0-6.8)
China	13.5	91.3 (90.8- 91.7)	98.5 (98.2- 98.7)	4.7 (4.3-5.1)
Philippines	38.5	72.0 (69.3- 74.9)	91.8 (89.7- 93.5)	4.3 (3.2-5.5)
Brazil	13.8	94.2 (93.8- 94.6)	98.3 (97.9- 98.5)	4.0 (3.4-4.6)
Australia	22.5	85.7 (84.1- 87.3)	98.7 (98.5- 98.9)	3.2 (2.7-3.7)
Mexico	27.6	91.1 (90.5- 91.7)	98.6 (98.3- 98.9)	3.0 (2.5-3.5)
Indonesia	4.7	91.5 (90.0- 93.3)	99.8 (99.7- 99.8)	2.7 (2.1-3.3)
Congo, Democratic Republic of the	71.7	86.1 (84.5- 87.7)	97.9 (97.5- 98.2)	2.4 (1.9-2.8)
Ecuador	46.2	88.1 (86.4- 89.8)	96.6 (95.1- 97.9)	1.4 (0.9-1.8)
Vietnam	14.3	90.8 (89.5- 91.9)	99.6 (99.4- 99.7)	1.4 (1.1-1.7)

*Notes: Same value attained for the projected and national scenario, because achieving projected country-specific production gain was an assumption in the national scenario.

Figure captions

Figure 1. Illustration of the methodological approach and data sources (a) Input land-use layers used to calculate current, attainable and projected crop production, and intensification levels. (b) Calculation of current crop production *Pc*, attainable crop production *Pa* when fully closing yield gaps and their difference (production gap ΔP). (c) Calculation of projected crop production *Pp* if yield gaps would be fully closed in all cells with projected intensification by 2040 under the OECD Environmental Outlook. (d) Calculation of global habitat fractions within agricultural lands *H* and cropland (*SC*) and non-cropland proportions of suitable habitat (*SN*). (e) Species' likelihood to persist at a given crop-specific intensification level. Crop-specific intensification levels were derived from current (*Ic*) or projected fractions of attainable yields achieved (*Ip*), and for non-cropland proportions of suitable habitat additionally multiplied with the total cropland proportions of agricultural lands *C*. For each species, random response functions were generated from the assumed possible responses to agricultural intensification. The species' likelihood to persist, summed over the cropland and non-cropland proportions of suitable habitat, was multiplied by the crop-specific growing area share *GA* to optimize intensification for each crop separately. (f) Calculation of the crop-specific biodiversity value of agricultural lands *B* from the elements described in (d) and (e) and its change when fully closing yield gaps (biodiversity loss ΔB). (g-j) Calculation of intensification-biodiversity trade-offs to derive crop-specific priority sequences for intensification, and description of scenarios and questions addressed in this study.

Figure 2. Global biodiversity value retained in agricultural lands under three scenarios of agricultural intensification on existing croplands: i) OECD Environmental Outlook projections (Van Asselen & Verburg, 2013; gray line segments), ii) a national (orange) and iii) a global optimization scenario (purple). The results are shown when yield gaps can be

fully closed. The national scenario assumes that each country independently prioritizes the cells with the lowest national intensification-biodiversity trade-offs for intensification, until that country's projected production volume is achieved. The global scenario assumes a global coordination to prioritize cells with the lowest global trade-offs, regardless of country-specific production projections. The biodiversity values and production increases are relative to the baseline year 2000. Lighter shades and the error bar show the range of the predictions over 1000 model runs.

Figure 3. Concordance map of biodiversity loss and production gap when fully closing yield gaps (a) and national vs. global priorities for closing yield gaps while minimizing associated biodiversity loss under two optimization scenarios of agricultural intensification (b). In (a), biodiversity loss is calculated as the difference between the biodiversity values of agricultural lands in the baseline year 2000 and when fully closing yield gaps. The associated production gap is calculated as the difference between potential production when closing yield gaps and the production of the baseline year. Purple-colored areas show potential conflicts, i.e. areas with high biodiversity loss and a high potential for production gain when closing yield gaps. Values are grouped into quartiles. In (b), priorities are calculated as the proportion of maximum attainable calories realized over the sixteen most important crops in both scenarios when achieving globally projected production gains from agricultural intensification, and grouped into quartiles. Purple cells show areas prioritized in both scenarios. Cells containing croplands but which were not prioritized for intensification in any of the runs under either scenario are not colored. The maps are shown in Eckert IV projection, the world basemap was derived from Natural Earth (2016).

Figure 4. Country-level socio-economic and ecological implications of national- vs. global-scale land-use optimization between agricultural intensification and biodiversity conservation. (a) Production gains under the global optimization scenario divided by

production gains under the national scenario, when achieving globally projected production gains from agricultural intensification (*production ratio*), grouped into quartiles. Darker-colored countries would benefit from higher production gains in the global compared to the national scenario. (b) Biodiversity value retained in agricultural lands under the global scenario divided by the retained biodiversity value under the national scenario when achieving globally projected production gains from agricultural intensification (*biodiversity ratio*). Darker-colored countries would retain higher biodiversity values in the global compared to the national scenario. (c) Concordance map of production and biodiversity ratios between the global and national scenario when achieving globally projected production gains from agricultural intensification, grouped into quartiles. Purple-colored countries are both production and biodiversity 'winners' in the global scenario (high production gains with low biodiversity loss or low production losses with strong decrease in the biodiversity loss relative to the national scenario). Light grey colors indicate areas free of croplands or with missing data. (d) Development of global/national-scenario *production ratios* for selected countries along increasing global intensification-driven production levels. (e) Development of global/national-scenario *biodiversity ratios* for selected countries along increasing global intensification-driven production levels. Global production increases in (d) and (e) are relative to the baseline year 2000. Black lines show the mean, grey areas the range of predictions over 1000 model runs. BWA = Botswana, GBR = United Kingdom, IND = India, NIC = Nicaragua, RUS = Russia, USA = United States of America. The maps are shown in Eckert IV projection, the world basemap was derived from Natural Earth (2016).

Supporting information

Filename: Figures_1_2_Tables_1_4_Supp.docx

Format: Word document

Description:

Fig. S1 Global biodiversity value retained in agricultural lands under scenarios of nationally and globally optimized agricultural intensification.

Fig. S2 Uncertainty of national vs. global priorities for closing yield gaps while minimizing associated biodiversity loss under two scenarios of agricultural intensification.

Table S1 Datasets used in this study.

Table S2 Definition of habitat categories based on preferred habitat types and their assignment to the land-cover classes.

Table S3 Minimum, central and maximum functions defining spaces of species' possible responses to agricultural intensification.

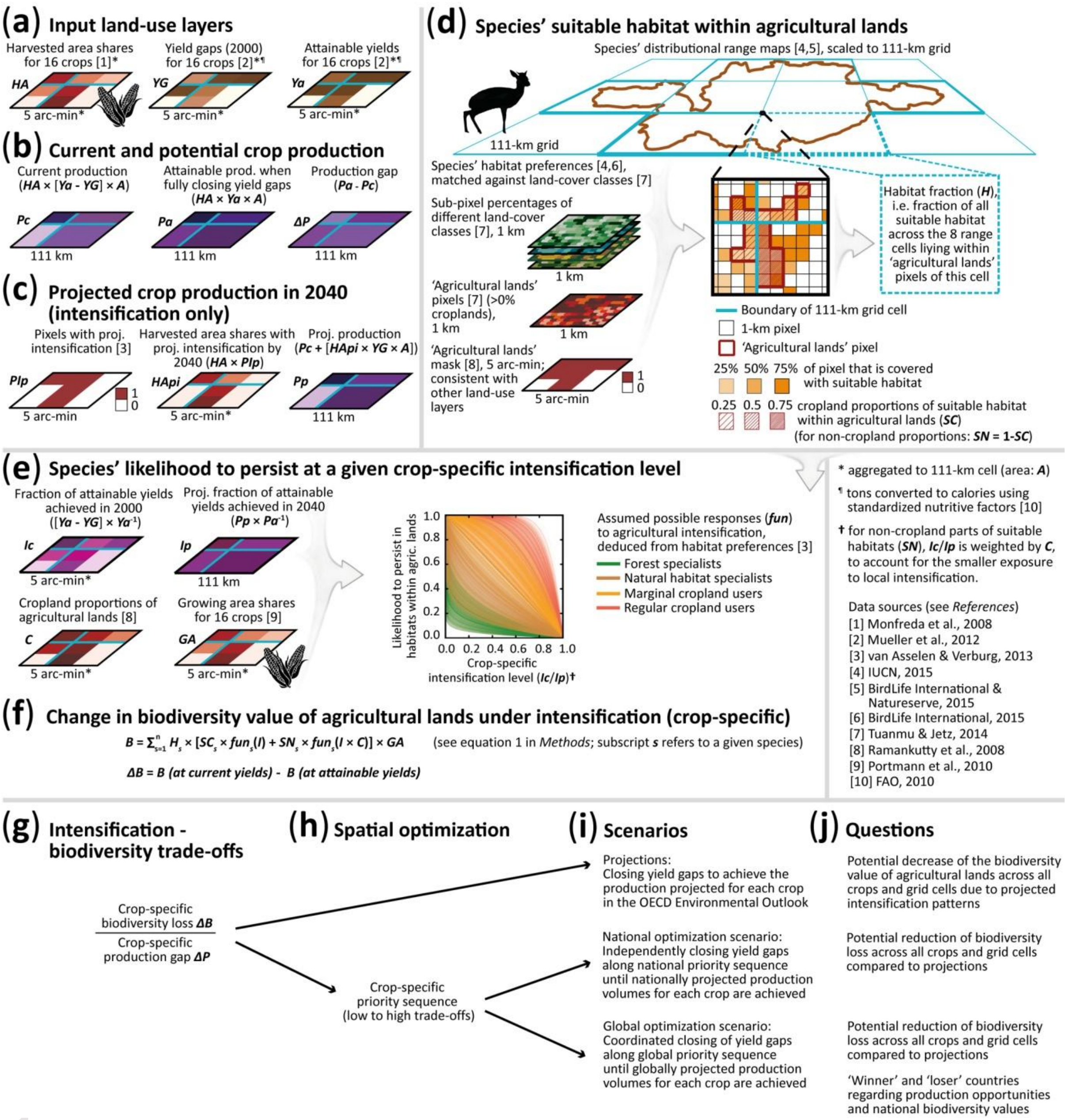
Table S4 Crop-specific production gains and biodiversity values.

Filename: Table_5_Supp.csv

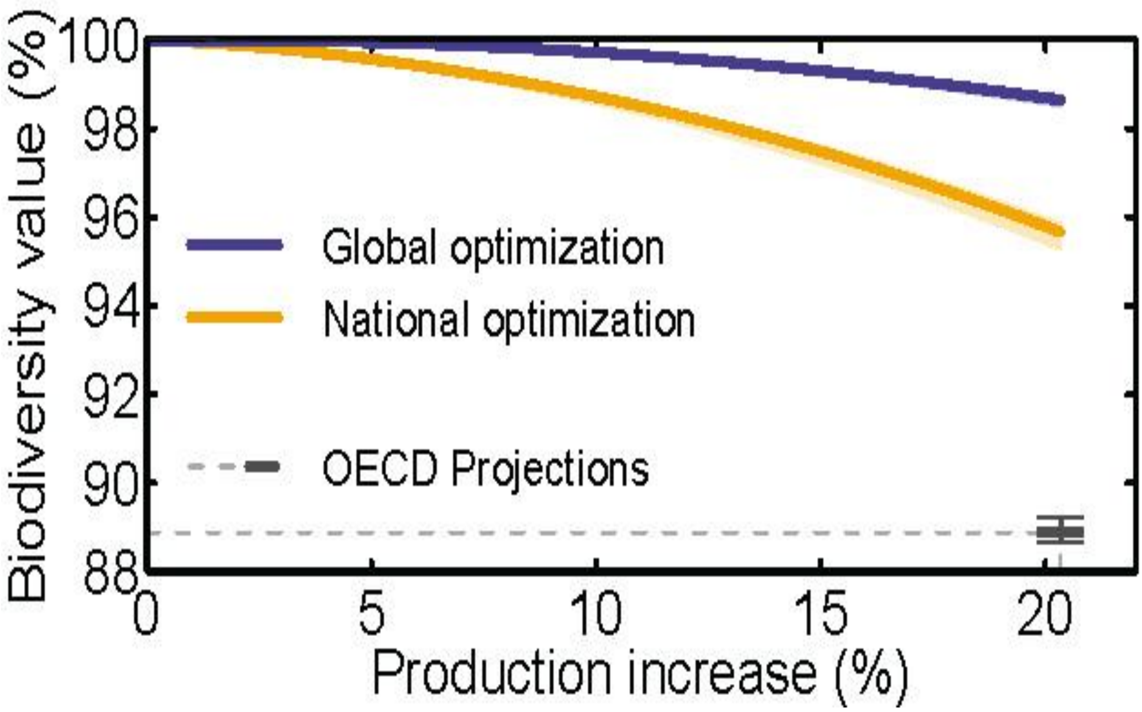
Format: Excel document

Description:

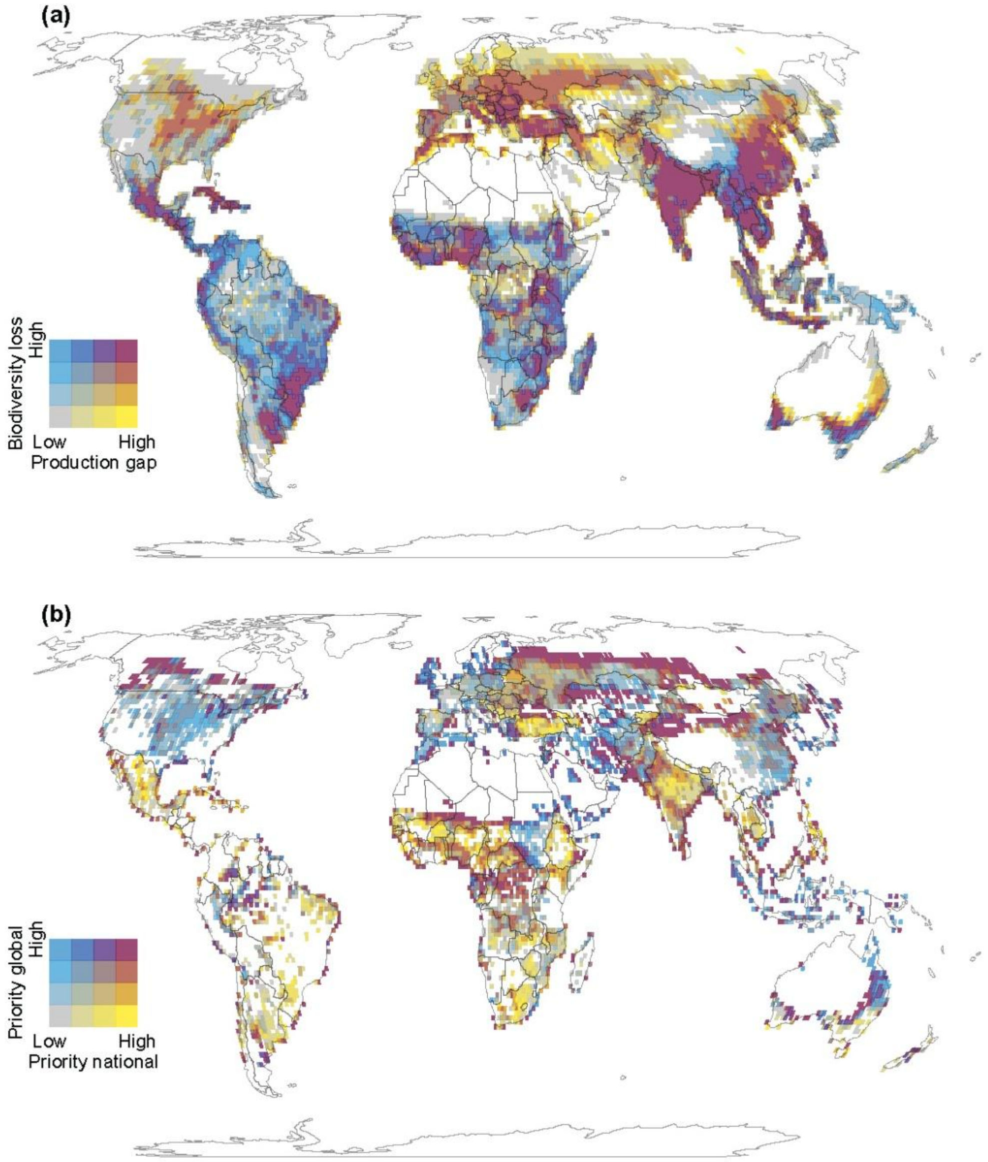
Table S5 Country-specific production gains and biodiversity values. Column 2-3 indicate the country-specific production gains relative to the baseline year 2000 under the projections/national scenario and under the global scenario, column 4 the biodiversity value in the baseline year (absolute), and columns 5-7 show the relative biodiversity value retained under three scenarios of agricultural intensification on existing croplands relative to the baseline value; projections under the OECD Environmental Outlook, a national and a global optimization scenario. Column 8 indicates the estimated relative avoidance of the projected global biodiversity loss under the national optimization scenario (difference between optimized and projected biodiversity value on the national level divided by the globally projected biodiversity loss). Columns 9-10 show the relative production gain and biodiversity value when yield gaps are fully closed (full intensification) relative to the baseline year 2000. Values in brackets indicate the range of the predictions over 1000 model runs. Note: projected global biodiversity loss avoided under the national scenario is below 0.0% for many countries, while these countries often retain substantially higher biodiversity values under the national scenario compared to the projections.

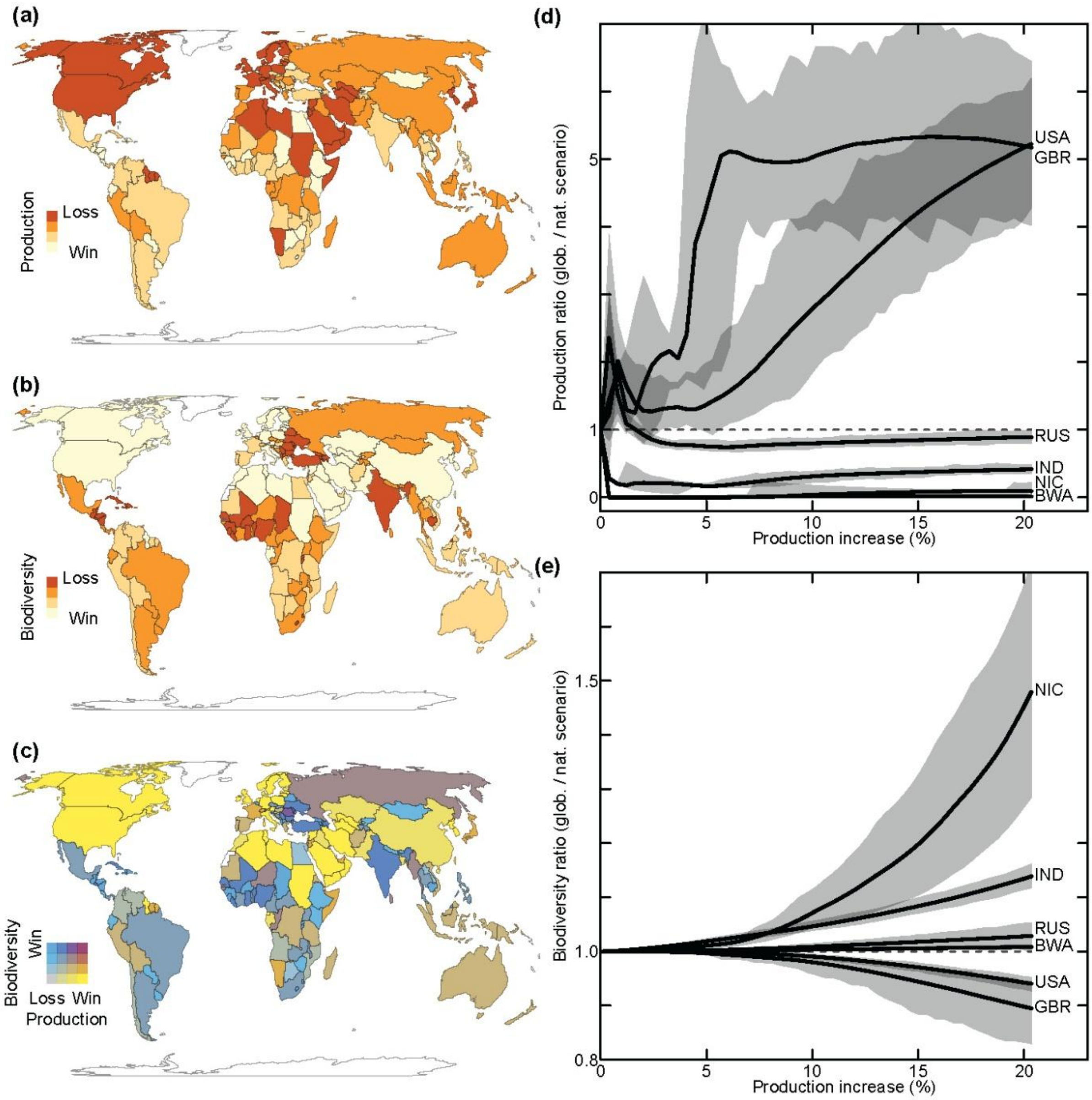


(a) Input land-use layers
Harvested area shares for 16 crops [1]*
Yield gaps (2000) for 16 crops [2]*¶
Attainable yields for 16 crops [2]*¶
HA
YG
Ya
5 arc-min*
5 arc-min*
5 arc-min*
(b) Current and potential crop production
Current production (HA × [Ya - YG] × A)
Attainable prod. when fully closing yield gaps (HA × Ya × A)
Production gap (Pa - Pc)
Pc
Pa
ΔP
111 km
111 km
111 km
(c) Projected crop production in 2040 (intensification only)
Pixels with proj. intensification [3]
Harvested area shares with proj. intensification by 2040 (HA × PIp)
Proj. production (Pc + [HApi × YG × A])
PIp
HApi
Pp
1
0
5 arc-min
5 arc-min*
111 km
(d) Species' suitable habitat within agricultural lands
Species' distributional range maps [4,5], scaled to 111-km grid
111-km grid
Species' habitat preferences [4,6], matched against land-cover classes [7]
Sub-pixel percentages of different land-cover classes [7], 1 km
1 km
'Agricultural lands' pixels [7] (>0% croplands), 1 km
1 km
'Agricultural lands' mask [8], 5 arc-min; consistent with other land-use layers
5 arc-min
1
0
Habitat fraction (H), i.e. fraction of all suitable habitat across the 8 range cells lying within 'agricultural lands' pixels of this cell
Boundary of 111-km grid cell
1-km pixel
'Agricultural lands' pixel
25% 50% 75% of pixel that is covered with suitable habitat
0.25 0.5 0.75 cropland proportions of suitable habitat within agricultural lands (SC)
(for non-cropland proportions: SN = 1-SC)
(e) Species' likelihood to persist at a given crop-specific intensification level
Fraction of attainable yields achieved in 2000 ([Ya - YG] × Ya^-1)
Proj. fraction of attainable yields achieved in 2040 (Pp × Pa^-1)
Ic
Ip
5 arc-min*
111 km
Cropland proportions of agricultural lands [8]
Growing area shares for 16 crops [9]
C
GA
5 arc-min*
5 arc-min*
Likelihood to persist in habitats within agric. lands
1.0
0.8
0.6
0.4
0.2
0.0
0.0 0.2 0.4 0.6 0.8 1.0
Crop-specific intensification level (Ic/Ip)†
Assumed possible responses (fun) to agricultural intensification, deduced from habitat preferences [3]
Forest specialists
Natural habitat specialists
Marginal cropland users
Regular cropland users
* aggregated to 111-km cell (area: A)
¶ tons converted to calories using standardized nutritive factors [10]
† for non-cropland parts of suitable habitats (SN), Ic/Ip is weighted by C, to account for the smaller exposure to local intensification.
Data sources (see References)
[1] Monfreda et al., 2008
[2] Mueller et al., 2012
[3] van Asselen & Verburg, 2013
[4] IUCN, 2015
[5] BirdLife International & Natureserve, 2015
[6] BirdLife International, 2015
[7] Tuanmu & Jetz, 2014
[8] Ramankutty et al., 2008
[9] Portmann et al., 2010
[10] FAO, 2010
(f) Change in biodiversity value of agricultural lands under intensification (crop-specific)
B = Σ_{s=1}^{n} H_s × [SC_s × fun_s(I) + SN_s × fun_s(I × C)] × GA
(see equation 1 in Methods; subscript s refers to a given species)
ΔB = B (at current yields) - B (at attainable yields)
(g) Intensification - biodiversity trade-offs
Crop-specific biodiversity loss ΔB
Crop-specific production gap ΔP
(h) Spatial optimization
Crop-specific priority sequence (low to high trade-offs)
(i) Scenarios
Projections: Closing yield gaps to achieve the production projected for each crop in the OECD Environmental Outlook
National optimization scenario: Independently closing yield gaps along national priority sequence until nationally projected production volumes for each crop are achieved
Global optimization scenario: Coordinated closing of yield gaps along global priority sequence until globally projected production volumes for each crop are achieved
(j) Questions
Potential decrease of the biodiversity value of agricultural lands across all crops and grid cells due to projected intensification patterns
Potential reduction of biodiversity loss across all crops and grid cells compared to projections
Potential reduction of biodiversity loss across all crops and grid cells compared to projections
'Winner' and 'loser' countries regarding production opportunities and national biodiversity values



Biodiversity value (%)
100
98
96
94
92
90
88
Global optimization
National optimization
OECD Projections
0
5
10
15
20
Production increase (%)


(a)
Biodiversity loss
High
Low
High
Production gap
(b)
Priority global
High
Low
High
Priority national


(a)
Production
Loss
Win
(b)
Biodiversity
Loss
Win
(c)
Biodiversity
Win
Loss Win
Production
(d)
Production ratio (glob. / nat. scenario)
USA
GBR
RUS
IND
NIC
BWA
Production increase (%)
(e)
Biodiversity ratio (glob. / nat. scenario)
NIC
IND
RUS
BWA
USA
GBR
Production increase (%)