Limits to agricultural land for retaining acceptable levels of local biodiversity

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Abstract

Several studies have proposed maximum allowable areas of cropland (12.6-15.18% of terrestrial area) as environmental sustainability requirements, yet none have so far considered the minimum biodiversity levels required to support ecosystem functioning at acceptable levels. Here we use a decision tree-based optimisation model to estimate the maximum area of cropland and pasture that would meet, or would come closest to meeting, the acceptable levels of local biodiversity proposed in the literature (90% local species abundance, 80% local species richness compared to an undisturbed baseline). We model four scenarios in which we vary two key sources of uncertainty: the maximisation function and the potential of secondary vegetation to maintain biodiversity. The model finds that a maximum of 4.62-11.17% of the global ice-free land can be allocated to cropland (7.86-15.67% to pasture) to meet these biodiversity constraints, a lower level than suggested in previous studies. The results are very sensitive to the minimum acceptable biodiversity values and the biodiversity response factors used, but the size of the disparity between current cropland area and our results suggest that actions to limit or reduce the area dedicated to agriculture should feature more prominently in policy discussions.

The conversion of natural ecosystems for agricultural, residential, and industrial purposes has enabled the food and housing demands of a significant proportion of the world's population to be met, in addition to supporting the expansion of the global economy [1]. However, the relevance of land goes beyond market goods; it provides habitat for species and is central to the provision of many ecosystem services, such as carbon storage, water purification, etc. [2]

One land use often precludes another, so that the use of land inevitably leads to economic, social and environmental trade-offs. So far, the provision of goods with market value has taken priority over ecosystem services that may be undervalued or not valued at all [3,4], which leads to a suboptimal allocation of land resources [5]. As a result, land use change is currently one of the main drivers behind biodiversity loss [6] as well as an important contributor to climate change [7,8] and other key processes linked to changes in the functioning of the Earth system [9].

Maximum acceptable areas of cropland and minimum values for biome-specific forested areas have been proposed to safeguard the integrity of the biosphere (left side of Figure 1). Maximum proposed areas of cropland range from 12.60% to 15.18% of global ice free land [10-13] (current value is 12.13% [14]) (more details can be found in the supplementary material). Proposed values for minimum forested areas are in the 50-85% range of potential forest depending on the biome [15].

The maximum cropland coverage values above aim to limit biodiversity loss or maintain climate regulation, but are all based on expert estimates and do not consider minimum biodiversity levels required to support ecosystem functioning. Heck, et al. [13] also considers future food demand and water scarcity, but biodiversity is represented only by an indicator of risk of species loss at biome level without a reference sustainable value. This raises the question of whether previous estimates of maximum cropland area are consistent with minimum acceptable biodiversity levels proposed elsewhere [15,16]. In this context, Steffen, et al. [15] argued that the minimum biodiversity and forest cover requirements would almost certainly be consistent with each other but offered no quantitative proof.

Here, we present the first analysis that sets targets for the maximum allowable cropland area that has the potential to maintain biodiversity within proposed acceptable levels. Such levels are here defined as 90% of naturally occurring local species abundance (number of individuals) and 80% of naturally-occurring local species richness (number of species). The 90% abundance threshold was proposed as a precautionary safe level, while acknowledging that the value could vary widely and be as low as 30% in circumstances [15]. 20% of species loss was considered to significantly affect certain ecosystem functions [16]. Both values refer to local biodiversity loss relative to an undisturbed state and are used as a proxy for the maintenance of key functions and ecosystem processes.

We undertake our analysis in two steps. First, we calculate biodiversity loss in 2015 relative to an un-impacted baseline. To do so, we build on work by Newbold, et al. [17] to combine the biodiversity response factors derived from a comprehensive ecological model that inferred past net changes in local species abundance and richness as a result of human pressures [18] with data on land use and land use intensity, which are major contributors to biodiversity loss. These factors describe the impacts of land use, land-use intensity, human population density and roads on local biodiversity, but are also likely to capture other relevant pressures implicitly – such as harvesting and invasive species [19,20] – e.g., harvesting pressure is likely to correlate with land use and distance to roads. In contrast to the original Newbold, et al. [17] study, we do not include the impacts of human population density and roads. The effects of climate change on local species diversity are also omitted in this study.

Land use and land use maps have been generated following Newbold, et al. [18] (see methods) and aggregated to subecoregion level. The resulting land use shares have been multiplied by the corresponding biodiversity response factors (see Table 1) to calculate the biodiversity loss in 2015 relative to an undisturbed reference. While the provision of ecosystem services operates at different spatial scales from local to global [21], we have chosen subecoregions – the subunits of the 867 terrestrial ecoregions [22] – as the units of analysis because these remain the smallest (and at the same time most restrictive) functional unit with an ecological meaning when modelling biodiversity around the whole globe. Ecoregions represent spatial units that represent relatively large areas of land containing a distinct assemblage of natural communities and species prior to major land-use change [22] and have been shown to effectively map global biodiversity patterns [23]. Thus, they can broadly be seen as a proxy for baseline ecosystem functioning.

In the second step, we derive subecoregion-specific maximum allowable cropland values by means of a decision tree-based optimisation algorithm that models the end state of possible land-use transitions that can achieve – or get as close as possible to – the minimum biodiversity requirements described above. To increase the representativeness of the results, we model two scenarios that either represent current food patterns (A: when maximising agricultural land, the proportion of cropland-to-pasture is kept constant) or a shift to a less land-intensive diet (C: we prioritise cropland over pasture in the maximisation function), where we implicitly assume that the percentage of crops used to feed animals would significantly decrease. These scenarios are further split based on the assumed potentials of secondary vegetation to retain local biodiversity values: short-term (0 years) and mid-term (30 years) (see methods for more details). This results in four scenarios: A0, A30, C0 and C30 that are used to explore reductions in agricultural land needed in the present to meet minimum acceptable biodiversity levels.

The optimisation model allows agricultural land to expand into productive land previously occupied by secondary vegetation when initial biodiversity levels are higher than the minimum requirements, or it allows agricultural land to be replaced by minimally-impacted secondary vegetation when initial biodiversity levels are too low. In both transitions, urban land and primary vegetation are kept fixed, as changes to the former and losses of the latter are irreversible [24]. Plantations also remain constant thereby assuming current demand levels for forest-based products. In cases where it is impossible to meet the minimum biodiversity requirements – e.g. in a subecoregion dominated by urban areas and plantations – the transitions modelled keep local biodiversity levels as close as possible to the minimum acceptable levels. The model assumes current exploitation practices in terms of intensity of land use.

The land-use transitions modelled are not intended to represent sustainable land futures in each subecoregion, as these transitions would negatively affect the provision of food; rather, the results should be seen as an attempt to capture the magnitude of the challenge from a biodiversity/land use perspective. We tested the sensitivity of the results to different assumptions in the biodiversity response factors, minimum acceptable biodiversity levels, the unit of analysis and time.

Results

Based on the land use composition in 2015, our results suggest that under current land use management practices, cropland could only cover between 4.62% and 11.17% of global ice-free land to potentially restore local biodiversity to suggested levels depending on the scenario. Under current dietary patterns (scenarios A0 and A30), cropland areas would be limited to the range 4.62-6.69% (11.20-15.67% for pasture). In contrast, a shift towards diets relying on less animal-based food products would open the window to 7.92-11.17% of global ice-free land for cropland (7.86-11.09% for pasture) (see Supplementary Figure 1). As a reference, in 2015 12.13% of land was allocated to growing crops, and 25.03% to pasture [14]. As shown in Figure 1, our estimate is substantially lower than previous maximum levels of cropland proposed in the literature. Thus, if our minimum acceptable biodiversity requirements are broadly correct, the challenge of keeping local species diversity at levels that are expected to ensure the long-term functioning of ecosystems has been underestimated. This challenge would not only entail reductions in global cropland area, but would also require a significant decrease in pasture. It should also be noted that previous estimates leave some room for cropland expansion, while ours do not, which shows that local biodiversity levels are lower than the minimum acceptable levels in many subecoregions, as reported previously [17]. For visibility purposes, the rest of the figures only show the results of one scenario: C30, the most optimistic scenario. C30 represents a shift towards less land-intensive diets and is therefore the most permissive scenario in terms of maximum cropland extension. The supplementary material shows the results for all the scenarios modelled.

INSERT FIGURE 1 HERE

As concluded by Newbold, et al. [17], the extent of cropland area is very sensitive to assumed biodiversity requirements (Figure 2). When relaxing the abundance and richness constraints from 90% and 80% to 80% and 71% respectively, the maximum cropland area increases to 20.22%; higher than the estimates from the literature. As mentioned previously, minimum acceptable species abundance could be as low as 30% at least in certain ecoregions. The results are also very sensitive to assumptions on biodiversity response factors as shown in the figure. In this case, our results also overlap with previous expert estimates.

The choice of subecoregions as unit of analysis can also be subject to uncertainties, considering that ecosystem services operate at different scales [21]. Figure 3 in the supplementary material shows the maximum cropland area after solving the model at different spatial scales. While differences from solving at subecoregion and ecoregion scales are negligible, using bigger units of analysis such as the combination of biogeographic realms and biomes results in higher maximum global cropland values. Nonetheless, these are still lower than current cropland values in three out of the four scenarios. Thus, the results are not very sensitive to the unit of analysis used.

Because maximum allowable cropland area depends on the initial land use arrangement, we also tested the sensitivity of the results to time. Over the last 15 years, maximum allowable cropland has barely changed (Supplementary Figure 4).

INSERT FIGURE 2 HERE

Maximum allowable cropland area varies across subecoregions. Hence, the sustainability gap – i.e. the difference between current cropland area and the maximum cropland area that would meet the biodiversity target (expressed as a %) – is subject to spatial variations. Figure 3 displays the sustainability gap as a percentage of maximum allowable cropland area, while Figure 4 shows the sustainability gap as a percentage of total area. Figure 3 indicates that the vast majority of subecoregions are already biotically compromised as a result of transgressing the reference value. In most cases, the transgression is quite severe, which represents the degree of unsustainable land use patterns in those areas. This suggests that significant reductions in cropland area would be required to create the necessary conditions for local species abundance and richness to potentially recover to acceptable levels. According to this analysis subecoregions in areas such as central Africa and the Amazon could – in theory – be allowed some increase in the area dedicated to agriculture without transgressing minimum acceptable biodiversity levels but this should not be considered seriously given the importance of these areas for earth system stability [25] and other evidence showing a dramatic loss of species abundance in the tropics [26]. In absolute terms, i.e. compared to total land in the subecoregion, the potential for expanding cropland in these regions is rather limited (Figure 4) and would come at the expense of other ecosystem services such as carbon storage.

INSERT FIGURE 3 HERE

INSERT FIGURE 4 HERE

It has been claimed that meeting the minimum acceptable biodiversity levels would comply with the minimum forest cover required to avoid dangerous climate tipping points [15]. We tested this hypothesis by estimating the maximum and minimum forest coverage resulting from the optimisation model (Figure 5) (see Methods). While improvements could be expected when meeting the biodiversity targets, these do not necessarily deliver the minimum forest coverage values proposed. Temperate forests would remain in the safe zone. However, for tropical and subtropical forests, maximum values would not reach the safe zone. Forested areas could also decrease in boreal forests and move away from the safe to the risk zone, since there is room for expanding agricultural areas without transgressing the minimum acceptable biodiversity levels.

INSERT FIGURE 5 HERE

Discussion

Our estimates link land use and land use intensity to local biodiversity loss using outputs from PREDICTS [18], the most comprehensive global model to date that represents local biodiversity changes associated with human pressures. In contrast to previous attempts, we relate changes in cropland area to minimum acceptable local biodiversity levels, carry out additional sensitivity analysis and consider the multifunctionality of land in terms of both local biodiversity and climate regulation (forest cover). Here we model the impacts of land use on local biodiversity and aggregate these results globally. We do not model global biodiversity. In theory, we could meet the local biodiversity requirements across subecoregions, while still losing many rare species globally [27]. We frame the discussion around five main statements:

- Statement 1: Previous estimates for maximum allowable cropland, based on expert assessment, are all less restrictive than our analysis suggests

Patterns that resemble current diets (modelled through the A0 and A30 scenarios) would leave little room for cropland area (4.62-6.69% of global ice-free land). Scenarios that represent a move towards less land-intensive diets (C0 and C30) suggests that a maximum of 7.86-11.09% of global cropland area gets closest to the minimum acceptable local biodiversity levels proposed in the literature. All these values are well below previous estimates of maximum cropland, which range from 12.60% to 15.18% of global ice-free land. In every scenario modelled, massive reductions in pasture land are required (7.86-15.67% of maximum global ice-free land; current value 25.03%).

- Statement 2: The maximum allowable cropland area is subject to relevant regional disparities

In controlling for local biodiversity loss, our optimisation model derives subecoregion-specific maximum values for cropland. This suggests that should there be a maximum allowable global level for agricultural land, this would be heterogeneous. While Rockström, et al. [10] acknowledged these caveats when proposing a maximum value, all existing estimates except that of Heck, et al. [13]

have been used as an homogenous maximum global cropland level [10-12] or have been downscaled to the national level in a straightforward way [11,28-30]. Although the use of aggregate figures can help communication, our analysis shows that it can potentially mask relevant regional disparities.

- Statement 3: Current cropland area is considerably higher than the maximum allowable value

Our results suggest that most subecoregions throughout the globe are biotically compromised as a result of land-use pressures. Consequently, large reductions in cropland area are needed in order to set the conditions necessary to potentially restore local species diversity to the minimum acceptable level proposed to ensure the long-term functioning of ecosystems. Figure 3 and Figure 4 highlight Europe, parts of North America, India and Central Africa as the regions that require greatest reductions in cropland. At the same time, there seems to be some potential for expanding cropland areas in the Amazon and boreal areas. This latter statement however needs qualification on three counts. First, although on average our estimates for local biodiversity levels are above the minimum proposed, the expansion of agricultural land would compromise other key ecosystem services such as carbon storage, and threaten existing rare species [31]. Second, the PREDICTS database from which the biodiversity response factors were obtained is based on very unevenly distributed case study data. This could potentially understate the impacts of land use and land use intensity in underrepresented areas such as the tropical forests, as recent findings suggest [26,32]. Third, Figure 3 suggests that in some areas such as Madagascar or the Mata Atlântica significant reductions in cropland are not required. This is because the model finds a solution after substantially decreasing pasture. The additional figures in the supplementary material should help contextualise these findings.

In an attempt to represent current management practices, the model assumes that primary vegetation, urban land and plantations, as well as the exploitation intensities of secondary vegetation and agricultural land remain constant. Thus, the results put in perspective the scale of the transformation needed, rather than delineate a transformation pathway. Bridging this gap seems challenging considering expected expansion of urban areas, which often takes place on productive agricultural land [24,33], the additional pressure future food and energy demand are expected to put on the land [34-36] and the potential effects of climate change on biodiversity [37].

- Statement 4: Reaching minimum acceptable biodiversity levels would not necessarily comply with the minimum values for global and biome-specific forested areas proposed for climate regulation

Steffen, et al. [15] hypothesised that achieving the minimum biodiversity levels fed into our model would push the tropical, subtropical, temperate and boreal forests towards the safe zone in Figure 5. While it is possible to meet the minimum acceptable biodiversity levels while moving to the safe forest zone, our results indicate that both situations do not necessarily go hand in hand. Uncertainty around safe forest cover levels is nonetheless significant.

- Statement 5: The results of the model are very sensitive to assumptions on minimum acceptable biodiversity levels and local biodiversity response factors

Our estimates are very sensitive to assumptions on minimum acceptable biodiversity levels that are still very uncertain. At this point, the 90% local species abundance target and the minimum forest requirements represent expert-driven estimates with limited scientific validation and high uncertainty [15,38]. Acceptable values should be defined at additional geographical levels after considering the variation in ecosystem functions, ecosystem dynamics at different spatial scales and the locally distinctive biotic components. All this remains an elusive task and a research priority.

At the same time, our analysis does not cover the impacts that achieving minimum species diversity levels would have on biomass production for human use. Compliance with minimum acceptable biodiversity levels in every subecoregion would demand a significant decrease in the exploitation of the most fertile available agricultural land and therefore affect food production. For this reason, the perspective analysed here does not necessarily represent the socially-desirable point. Recognising that there are trade-offs among different ecosystem services [39,40], decision makers will need to make judgements about what should be prioritised in different areas. Such a discussion is beyond the scope of this paper but it needs to take into account the constraints that our analysis reveals.

The results have also proved to be very sensitive to biodiversity response factors, as shown in Table 1. The biodiversity response factors used here assume a single global response of biodiversity to land use. However, effects of land use are known to vary across broad geographic regions [41,42], some of which are underrepresented in the case studies of the version of the PREDICTS database from which the response factors have been obtained, and depend on local land-use management practices [43,44]. Likewise, the results reflect net changes on biodiversity as expressed by the response factors and therefore do not consider the dynamics in community composition during the land use transitions modelled. Future studies like this should account for the variability of land-use impacts on biodiversity. The results should be interpreted in the light of these assumptions.

Conclusions

This exploratory study provides a first approximation of the challenge land-use planning faces in order to potentially restore local biodiversity to levels proposed in the scientific literature. Our results suggest that previous research has understated the significance of the land-use problem from a local biodiversity perspective.

The analysis presented here has identified areas that merit further detailed investigation. Because of the assumptions in the model, and the uncertainties in placing minimum acceptable biodiversity levels and of biodiversity response factors, we cannot draw definitive conclusions, but rather highlight the magnitude of the challenge ahead. For this reason, our results should not be used to guide biodiversity conservation and land use planning policies at regional or local levels. Such actions should be tailored to the local context and evaluate potential trade-offs of interventions considering both the material and immaterial services provided by ecosystems.

Nonetheless, we believe we can provide relevant insights at higher scales. The gap between current cropland levels and the maximum acceptable level we estimated is large enough to suggest that absolute reductions in cropland and pasture area are necessary in some subecoregions to reverse local biodiversity loss trends and ensure the long-term functioning potential of ecosystems. How such measures can be reconciled with feeding the growing world population and the optimism around using cropland for bio-energy with carbon capture and storage is a complex problem. Irrespective of this and while science tries to resolve this conundrum, the idea of reducing the area dedicated to agriculture should feature more prominently in policy discussions related to land use planning and the future of food systems.

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Author contribution

Concept, data and original draft: A.U.L.; Review and editing: A.U.L., G.M. and P.E.; Supervision: P.E.

Competing interest statement

The authors declare no conflict of interest.

Method

Our analysis estimates the maximum amount of cropland area that would be compatible with keeping biodiversity at minimum acceptable levels under different assumptions. These levels are the same biodiversity loss references adopted by Newbold, et al. [17], i.e. 10% and 20% local species abundance and richness loss respectively. We followed three steps: generating subecoregion-level land use and species diversity maps, building the decision tree-based optimisation model and testing the sensitivity of the results to biodiversity response factors, minimum acceptable biodiversity levels, unit of analysis and time.

Subecoregion-level land use and species diversity maps

We build on the work of Newbold, et al. [18] to generate maps of land use and land use intensities for each year in the period 2000-2015 at a 0.25° x 0.25° spatial resolution. Human population density and distance to roads, which were included in the original paper are not covered in this study because their effects are not additive to those of land use and land use intensity, which is the main focus of this study. We used the Land Use Harmonizaion[2] (LUH2) database [14] as a base map and grouped the available land-use categories into eight classes: cropland, pasture, urban, forested primary vegetation, non-forested primary vegetation, forested secondary vegetation, non-forested secondary vegetation and plantations. We eliminated the areas covered by water and/or ice. Sites were assigned an exploitation intensity level using van Asselen and Verburg [45] as reference, following the methods of Newbold, et al. [18]. Secondary vegetation was subdivided into age groups: young (<30 years), intermediate (30-100 years) and mature (>100 years) based on age data available in LUH2. In order to test sensitivity to assumptions at a later stage, we also generated maps in which instead of directly using current age data for secondary vegetation, we added 30 years to each relevant grid cell to reflect the potential of secondary vegetation to maintain biodiversity in the mid-term. This assumes, for instance, that current young secondary vegetation will behave like intermediate secondary vegetation in the mid-term. We overlaid the land use and land-use intensity data with a map of terrestrial subecoregions [22] before calculating species diversity levels in each subecoregion. The operations to manipulate spatial data were performed with the Python arcpy module for ArcGIS 10.4 [46].

For each subecoregion, mean relative species abundance and richness compared to undisturbed circumstances were calculated by multiplying the total proportional area of each land use within the subecoregion by the biodiversity response factors displayed in Table 1. This approach does not consider potential biases related with scaling up local biodiversity data to higher levels [47]. The response factors have been obtained from the 2015 release of the PREDICTS model [18]. The dataset contained 1,130,251 records of abundance and 320,924 of occurrence or species richness at 11,525 sites representing 26,953 species and 13 of the 14 terrestrial biomes.

INSERT TABLE 1 HERE

We also identified areas that would allow further cropland, pasture and forest expansion. Areas suitable for crop cultivation were defined using a yield gap map from FAO and IIASA [48] that showed the ratio of actual and potential yield for all main crop categories. All areas with a positive yield gap were considered potentially productive. We used FAO [49] to define areas suitable for pasture. Those with very low suitability were not considered further. Out of all the areas suitable for cropland and pasture, only those overlapping with secondary vegetation in the base map were considered for further expansion, thereby excluding potential expansion in primary vegetation, urban areas and plantations. For potential forest expansion, we used the data on potentially forested areas available in LUH2. LUH2 uses a global terrestrial model to differentiates between forested and non-forested areas. Areas with an aboveground standing stock of natural cover of at least 2 kg C m^{-2} are identified as potential forest [50].

All the relevant spatial data was aggregated at subecoregion level and rearranged as a table that served as input in the next step. In the table, columns represent the land use / land use intensity combinations in Table 1 and rows represent subecoregions. To populate the table, we aggregated the spatial data of each subecoregion into single vectors that reflect land use shares. We also aggregated data that was used as a constraint in the next steps to fit the same resolution (e.g. areas into which forest, cropland and pasture can expand).

Optimisation

We created a linear optimisation model in Python that describes the end state of possible land-use transitions in each subecoregion that maximize agricultural area, while meeting (when possible) minimum acceptable species diversity levels. When achieving the minimum biodiversity levels is not possible, the model tries to get as close to them as possible by reducing cropland and pasture to zero if necessary. Because the biodiversity indicators used represent relative local abundance and richness, there is no implicit judgement over the importance of some subecoregions in absolute biodiversity terms over others, despite the heterogeneity in species composition in ecoregions and land use types.

The optimisation model works as a decision tree. It is arranged in sequential conditional statements that describe the characteristics of each possible transition. For each subecoregion, the model identifies the appropriate transition based on initial parameters (e.g. initial biodiversity levels; available cropland, pasture and forested areas; cropland, pasture and forest potential) and calculates the net marginal change in species abundance and richness of the corresponding transition. The net marginal change shows how biodiversity would change when switching one unit of land use *a* by one unit of land use *b*. Then it determines the optimum level of change in land use that would lead to meeting the minimum acceptable biodiversity levels defined earlier or, when not possible, it calculates the point that would get closest to doing so. The solution is found exogenously based on straightforward linear algebra equations. Thus, the model is not a classical optimisation model and therefore does not require a built-in solver. The code can be made available for replication purposes.

Figure 6 and Figure 7 describe the decision tree on which the general functioning of the model is based. These figures distinguish two main land use transitions depending on whether minimum species abundance and richness levels are met in an subecoregion in the base year.

When initial biodiversity values are higher than the lowest acceptable levels, the model allows agricultural land to expand into productive land previously occupied by secondary vegetation as long as minimum biodiversity levels are maintained. This excludes agricultural land expansion into primary vegetation, plantations and urban areas. Expansion is not possible when secondary vegetation in the base year equals zero or when the conditions of the ecosystem are not suitable for additional agricultural land. The code can be made available for replication purposes.

Figure 6 and Figure 7 represent two slightly different possibilities for this transition. The former (C) gives priority to cropland expansion, i.e. pasture land can only expand when cropland has achieved its maximum possible extension based on the suitability maps we referred to in the previous section. The latter figure (A) assumes that both cropland and pasture expand into secondary vegetation keeping the same proportion as in the original land use arrangement. The ratio between the two is determined by their potentials, i.e. if the potential expansion of cropland and pasture are 10% and 5% of the existing ecosystem area, the model uses a 2:1

ratio when increasing the area devoted to agricultural land. As for secondary vegetation, the model maintains the original proportions between young, intermediate and mature vegetation constant. The exploitation intensity shares (minimal, light and intense) are kept constant for agricultural land and secondary vegetation so that the transition resembles current management practices as much as possible. Absolute changes are constrained by the suitability of the ecosystem for agricultural land expansion and the area of secondary vegetation available in the initial conditions, subject to the minimum requirements of species diversity.

Nonetheless, the initial biodiversity levels are usually below those considered acceptable. When this happens, agricultural land is converted into minimally-exploited secondary vegetation until sufficient biodiversity levels are reached. This assumes – as a general rule of thumb – the absence of hysteretic behaviour, which in the model is interpreted as local biodiversity potentially recovering or getting close over time to the response values depicted in Table 1 after the disturbance ceases (in this case agricultural land being converted into secondary vegetation). In real life conditions, some ecosystems can undergo state shifts when excessive pressure is exerted on them [51]. At the same time, ecosystem recovery can be subject to recovery debts, i.e. interim reductions of biodiversity and related functions that might occur during the recovery process [52], such that the ecological characteristics do not necessarily recover to the initial levels [53], which in any case, could take long time periods [54]. Because of this assumption, the restoration process modelled here is considered to create the necessary conditions for species diversity to potentially recover to previous conditions. As in the previous case, we distinguish two possible transitions depending on whether priority is given to cropland (pasture decreases first, then cropland) or agricultural land (the original cropland-to-pasture ratio is kept constant). In both cases, agricultural land is converted into secondary vegetation. Here we distinguish two additional pathways depending on the time frame adopted (short- or mid-term). When focusing on the short-term potential of secondary vegetation to host biodiversity, we assume that agricultural land use is converted into young secondary vegetation. This would reflect the real conditions. Nevertheless, with time young secondary vegetation would mature and increase its potential to maintain biodiversity. Following this reasoning, for mid-term potential the biodiversity levels attributable to newly converted secondary vegetation are assumed to be those of intermediate-age secondary vegetation. As in the previous case, the same agricultural land use-specific intensities are used when modelling changes. This type of transition is constrained by available agricultural land and potentially forested areas. The model allows the expansion of secondary vegetation into agricultural land until either both species richness and abundance reach the minimum acceptable levels adopted or until agricultural land is set to zero. The latter instance represents the closest point an ecosystem can get to meeting the minimum acceptable biodiversity levels.

In order to test whether meeting (or getting closest to meeting) the biodiversity constraints at subecoregion-level would be compatible with the safe ranges of forested areas defined by Steffen, et al. [15] with regard to energy and water regulation, we have calculated the range of global forested areas yielded by each model run. The minimum forested area in each run is obtained by assuming that reductions in secondary vegetation take place in forested areas when possible and then in non-forested areas. Similarly, the model assigns increases in secondary vegetation to non-forested areas. The maximum forested area is calculated the opposite way, with potential forest expansion limited to potentially forested areas as defined in the original source [14]. The reader should note that because biodiversity response factors do not distinguish between forested and non-forested secondary vegetation, the model yields the same biodiversity result irrespective of how forested area changes.

Table 2 summarises the four base runs described in the previous paragraphs. The base runs use the 2015 land use maps, the minimum biodiversity levels described above and the mean response factors in Table 1. They differ in terms of the type of agricultural land use that is given priority when modelling transitions and the time horizon taken in relation to the potential of secondary vegetation to retain local biodiversity values.

INSERT TABLE 2 HERE

Maximum values for forested area in Figure 5 were estimated by assuming that whenever possible all secondary vegetation expansion was converted into forest (see above for a definition of potentially forested area). The minimum values are the results of assuming the opposite, i.e. that no secondary vegetation becomes forest.

Sensitivity analysis

Additionally, we tested the sensitivity of the output to four key parameters separately: biodiversity response factors, minimum acceptable biodiversity levels, functional unit and time. The full results from these local sensitivity analyses are in the supplementary material.

In order to test sensitivity to biodiversity response factors, we grouped land use categories in five groups (cropland, pasture, urban, primary and secondary/plantations) and assigned them high, average or low impact factor values. High biodiversity response factors were chosen by taking the average between the average and the upper bound of the values in Table 1, while low biodiversity response factors were derived by taking the average between the averages and the lower bounds. We refrained from taking the upper and lower bounds directly because it creates very unrealistic combinations, e.g. mature secondary vegetation being less adequate than intensively managed cropland for biodiversity conservation. This leads to 3^5 combinations that were tested for the year 2015.

For minimum biodiversity levels, we run 11 instances for the year 2015 using the biodiversity constraint in Table 3**Error! Reference source not found.**. In every instance we decrease the abundance and richness constraint by the same percentage compared to the zero run.

We also tested sensitivity to the functional unit chosen by using ecoregions and the combination of biogeographical realms and biomes as functional units. To this end, we aggregated the original input data into the optimisation model to fit those functional units and reran the model for the year 2015.

INSERT TABLE 3 HERE

Last, sensitivity to time was tested by running the model using all the annual land use maps covering the period between 2000 and 2015. During this period, global cropland and pasture area remained relatively constant (+4%, -4% respectively). This was not necessarily the case at subecoregion level.

Data availability

The datasets used to generate the land use / land use intensity maps at subecoregion level, as well as the biodiversity response factors are freely available in the sources referenced above. Additional data generated during and/or analysed during the current study is available from the corresponding author on reasonable request. The code can be made available for replication purposes.

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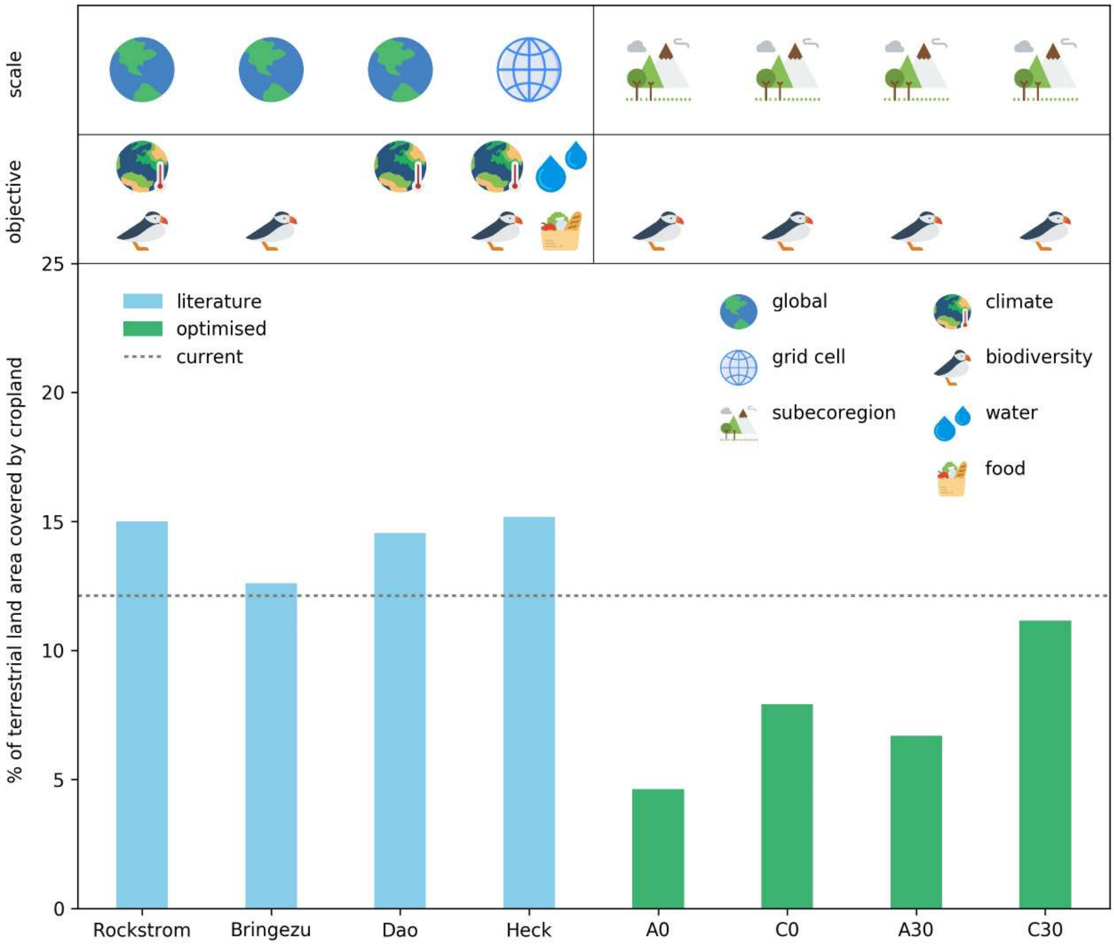
Figure captions

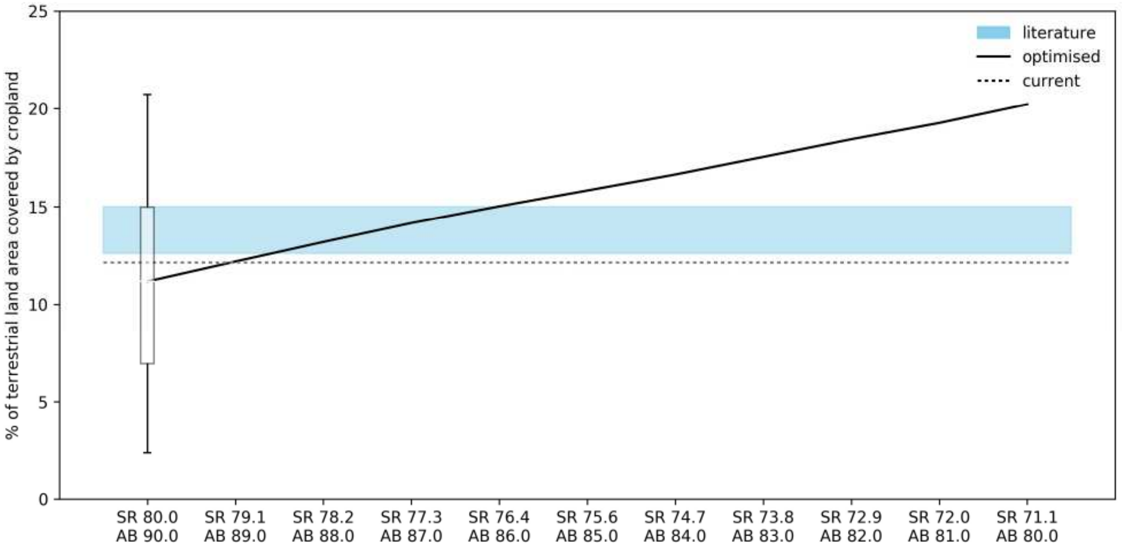
Figure 1: Comparison of maximum acceptable global cropland levels



The figure compares the results of the optimisation model with the reference values in the literature. Scenarios starting with A maximise agricultural land as a whole, while scenarios starting with C prioritise cropland over pasture when maximising agricultural land. The values on the right represent the potential of secondary land to maintain biodiversity (0: short- and 30: mid-term). The ‘scale’ parameter refers to the spatial unit of analysis, while the ‘objective’ parameter represents the environmental concern that the maximum cropland value is intended to address.

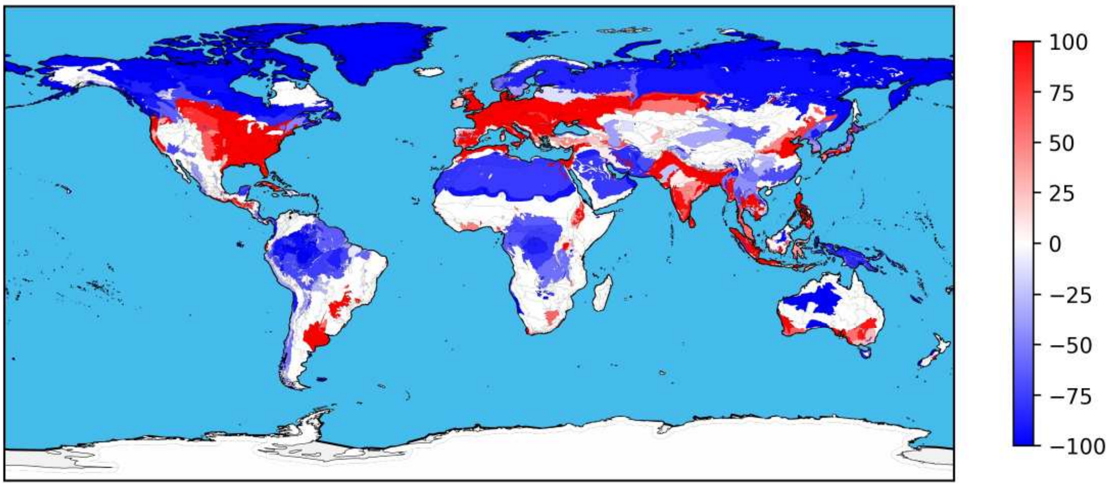
Icons made by Smashicons from www.flaticon.com

Figure 2: Sensitivity of maximum cropland levels to minimum biodiversity requirements and biodiversity response factors, 2015



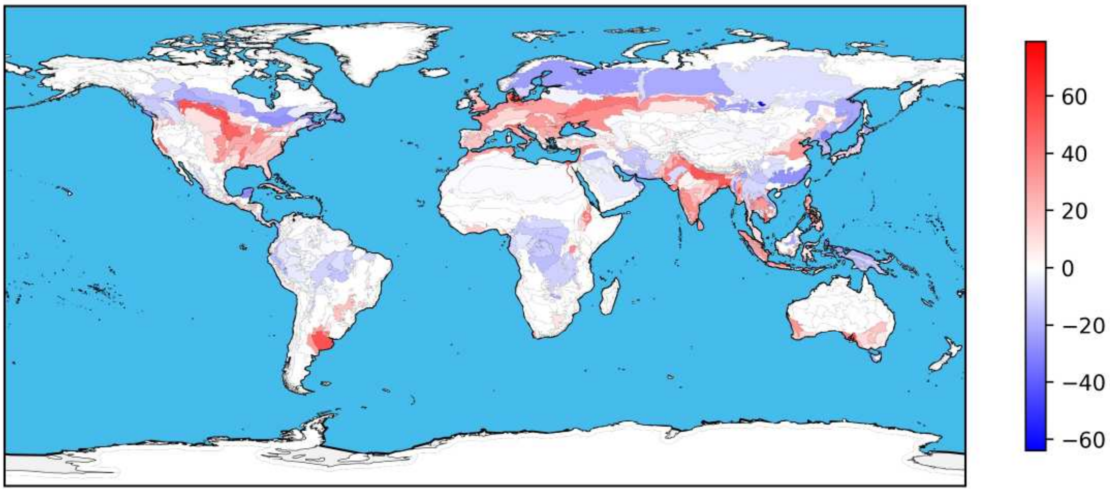
The figure represents the sensitivity of the results in scenario C30 to minimum acceptable biodiversity levels. AB and SR refer to species abundance and species richness respectively. The boxplot shows the sensitivity of the results in the base run to assumptions in the biodiversity response factors used. The upper and lower edges of the rectangle represent the 75th and 25th percentiles, while the top and bottom markers represent the maximum and minimum values. n = 243 in the boxplot.

Figure 3: Transgression of the sustainability gap in world subecoregions measured as the percentage of gap-to-reference, 2015



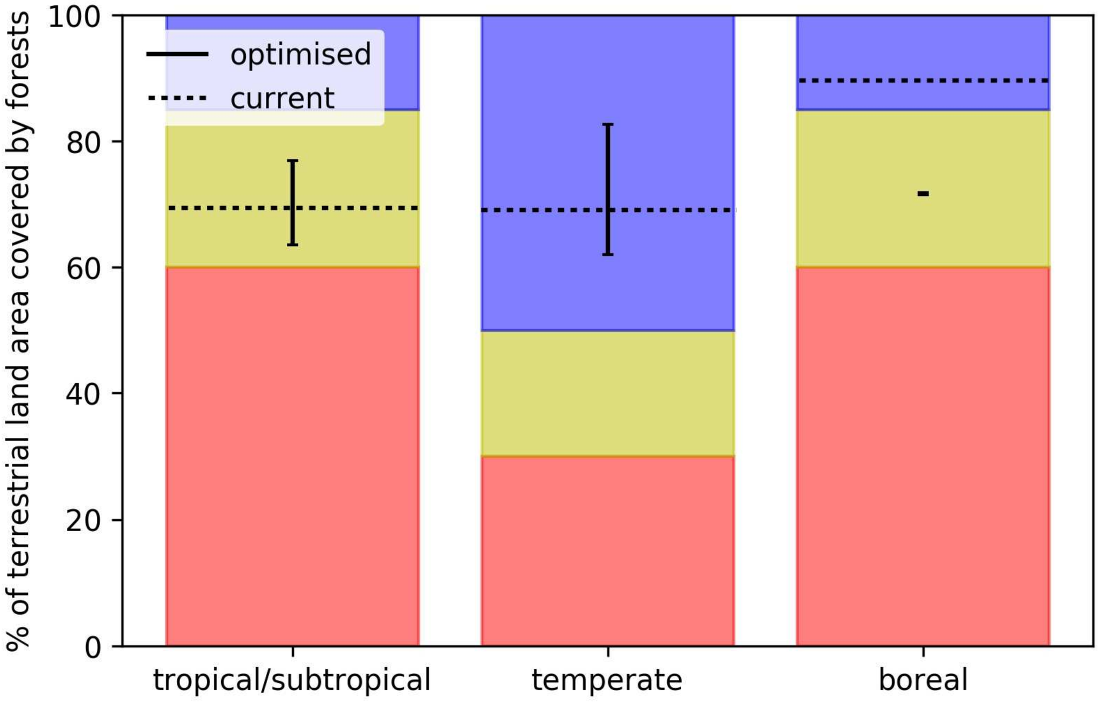
The figure shows the gap between cropland and maximum allowable cropland as a percentage of maximum allowable cropland for the scenario C30. For visibility purposes we have constrained positive gap-to-reference values to 100%. Red indicates that cropland exceeds the amount consistent with the biodiversity targets; blue indicates that the maximum allowable cropland to reach the biodiversity targets exceeds current cropland.

Figure 4: Transgression of the sustainability gap in world subecoregions measured as the percentage of gap-to-total land, 2015



The figure shows the gap between cropland and maximum allowable cropland as a percentage of available land for the scenario C30. Colour interpretation as in Figure 3.

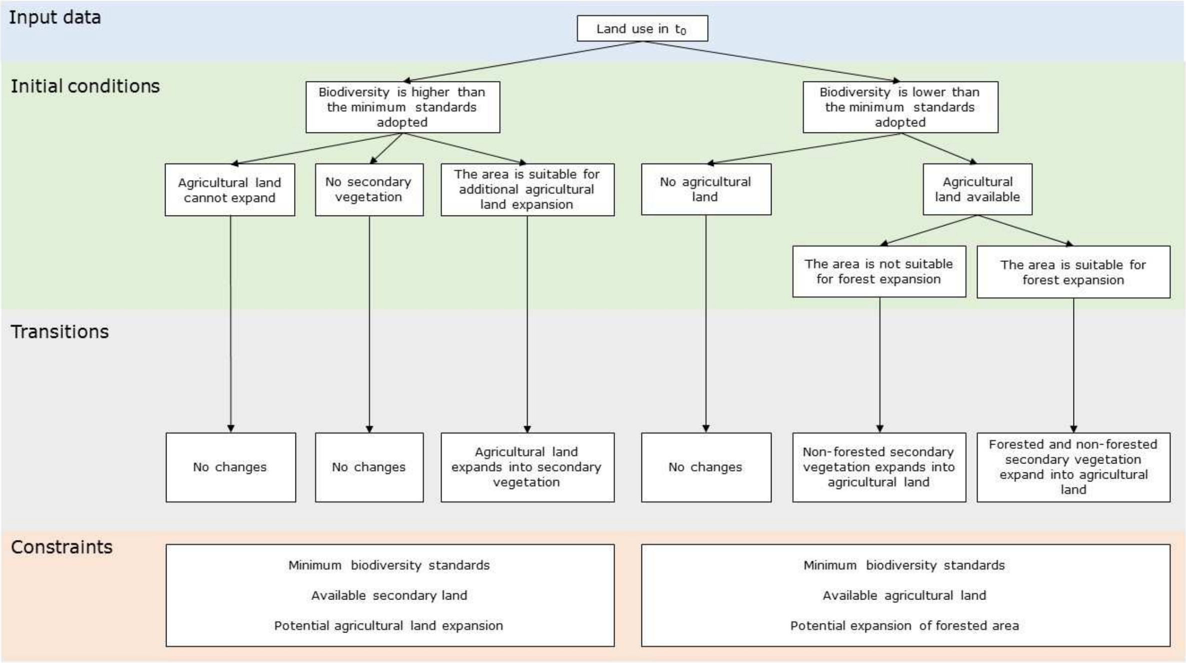
Figure 5: Forest cover in selected biomes in 2015 and under minimum acceptable biodiversity levels



The red, yellow and blue areas indicate the danger, risk and safe ranges for forest cover as proposed by

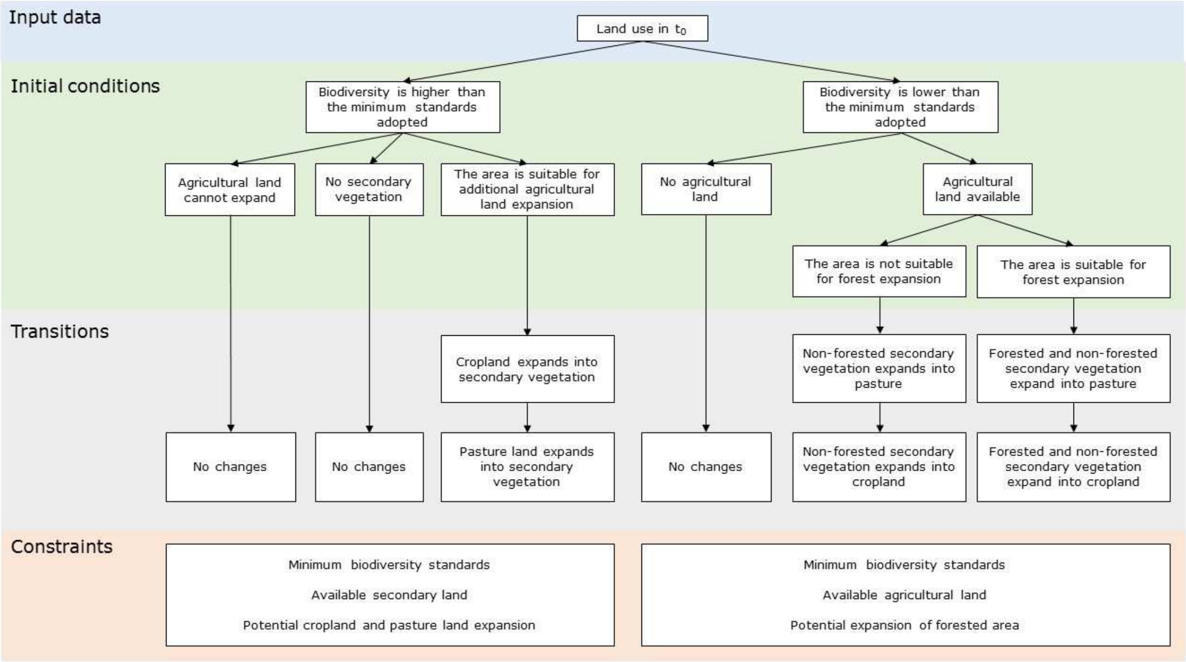
Steffen, et al. [15] based on the climate and water regulating function of forests. The straight vertical line indicates the maximum and minimum forest cover values obtained from the optimisation model in the base run of scenario C30. The horizontal dotted line represents current values for forested area. Current values slightly differ from those given in Steffen, et al. [15] because they are based on different sources.

Figure 6: Optimisation rules for the C scenarios (cropland takes priority over pasture)



Agricultural land comprises cropland and pasture. Primary and secondary vegetation can be forested or non-forested. Each land use category is split in the model according to its intensity as represented in Table 1.

Figure 7: Optimisation rules for the A scenarios (cropland and pasture expand and shrink in the same proportion as in t_0)



Agricultural land comprises cropland and pasture. Primary and secondary vegetation can be forested or non-forested. Each land use category is split in the model according to its intensity as represented in Table 1.

Tables

Table 1: Biodiversity response factors per land use type. Land use types with vegetation may be forested or non-forested.

Land use type	**Richness**	**Abundance**	**Land use type**	**Richness**	**Abundance**
Primary vegetation (Minimal use)	100	100	Plantation forest (Intense use)	60.6 (49.5-74.1)	95.7 (68.1-134.5)
Primary vegetation (Light use)	101.4 (94.6-108.6)	103.8 (88.9-121.3)	Cropland (Minimal use)	73.1 (64.0-83.5)	89.4 (69.2-115.4)
Primary vegetation (Intense use)	105.4 (92.5-120.1)	130.7 (98.9-172.8)	Cropland (Light use)	61.9 (52.4-73.2)	54.9 (40.1-75.1)
Mature secondary vegetation (Minimal use)	101.6 (90.2-114.5)	104.0 (82.2-131.4)	Cropland (Intense use)	63.7 (52.6-77.3)	68.7 (47.1-100.2)
Mature secondary vegetation (Light/intense use)	117.1 (99.0-138.6)	128.5 (85.3-193.6)	Pasture (Minimal use)	78.2 (67.8-90.1)	95.2 (73.6-123.1)
Intermediate secondary vegetation (Minimal use)	90.8 (82.2-100.2)	95.2 (78.3-115.7)	Pasture (Light use)	70.6 (61.3-81.2)	72.2 (56.0-93.0)
Intermediate secondary vegetation (Light/intense use)	90.1 (80.4-101.0)	76.6 (59.0-99.3)	Pasture (Intense use)	62.9 (50.8-77.9)	65.1 (44.1-96.0)
Young secondary vegetation (Minimal use)	84.4 (75.4-94.5)	89.0 (72.0-110.0)	Urban (Minimal use)	96.0 (79.4-116.0)	81.8 (51.6-129.7)
Young secondary vegetation (Light/intense use)	79.9 (68.8-92.7)	85.5 (64.0-114.2)	Urban (Light use)	65.3 (52.6-81.0)	55.1 (34.8-87.3)
Plantation forest (Minimal use)	80.8 (72.4-90.2)	113.4 (87.0-147.8)	Urban (Intense use)	49.8 (37.5-66.0)	37.6 (21.1-67.2)

Plantation forest (Light use)	73.1 (63.4-84.2)	77.8 (60.6-99.9)			

The table shows local species diversity response factors for abundance and richness compared to an undisturbed baseline. This is defined as primary vegetation with minimal exploitation intensity, zero human population density and away from major cities and roads. The first values represent the mean response to land use and land use intensity, while the values in parentheses indicate the 95% confidence interval. Forested and non-forested areas within the same land use category (e.g. primary, young secondary, intermediate secondary and mature secondary) have the same biodiversity response factors.

Source: Newbold, et al. [18]

Table 2: Main features of base runs

Code	Priority	Time scope	Year	Minimum biodiversity levels	Response factors
C0	Cropland	Short-term (+0 years)	2015	90% local species abundance compared to an undisturbed baseline 80% local species richness compared to an undisturbed baseline	Averages in Table 1
A0	Agricultural land				
C30	Cropland	Mid-term (+30 years)			
A30	Agricultural land				

Table 3: Minimum biodiversity levels used in the sensitivity analysis

Run	0	1	2	3	4	5	6	7	8	9	10
AB	90.0	89.0	88.0	87.0	86.0	85.0	84.0	83.0	82.0	81.0	80.0
SR	80.0	79.1	78.2	77.3	76.4	75.6	74.7	73.8	72.9	72.0	71.1

AB: species abundance, SR: species richness