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Spatial patterns of agricultural expansion determine impacts on biodiversity and carbon storage

Rebecca Chaplin-Kramer[a,1], Richard P. Sharp[a], Lisa Mandle[a], Sarah Sim[b], Justin Johnson[c], Isabela Butnar[b], Llorenç Milà i Canals[b], Bradley A. Eichelberger[a], Ivan Ramler[d], Carina Mueller[b], Nikolaus McLachlan[e], Anahita Yousefi[f], Henry King[b], and Peter M. Kareiva[g]

[a]Natural Capital Project, Woods Institute for the Environment, Stanford University, Stanford, CA 94305; [b]Safety and Environmental Assurance Centre, Unilever, Sharnbrook, Bedford MK44 1LQ, United Kingdom; [c]Department of Applied Economics, University of Minnesota, St. Paul, MN 55108; [d]Department of Mathematics, Computer Science, and Statistics, St. Lawrence University, Canton, NY 13617; [e]Department of Earth Sciences, University of Bayreuth, 95447 Bayreuth, Germany; [f]Ministry of Climate and Environment, 0030 Oslo, Norway; and [g]The Nature Conservancy, Arlington, VA 22203-1606

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The agricultural expansion and intensification required to meet growing food and agri-based product demand present important challenges to future levels and management of biodiversity and ecosystem services. Influential actors such as corporations, governments, and multilateral organizations have made commitments to meeting future agricultural demand sustainably and preserving critical ecosystems. Current approaches to predicting the impacts of agricultural expansion involve calculation of total land conversion and assessment of the impacts on biodiversity or ecosystem services on a per-area basis, generally assuming a linear relationship between impact and land area. However, the impacts of continuing land development are often not linear and can vary considerably with spatial configuration. We demonstrate what could be gained by spatially explicit analysis of agricultural expansion at a large scale compared with the simple measure of total area converted, with a focus on the impacts on biodiversity and carbon storage. Using simple modeling approaches for two regions of Brazil, we find that for the same amount of land conversion, the declines in biodiversity and carbon storage can vary two- to fourfold depending on the spatial pattern of conversion. Impacts increase most rapidly in the earliest stages of agricultural expansion and are more pronounced in scenarios where conversion occurs in forest interiors compared with expansion into forests from their edges. This study reveals the importance of spatially explicit information in the assessment of land-use change impacts and for future land management and conservation.

ecosystem services | deforestation | agricultural expansion | fragmentation | edge effects

Agriculture is a major contributor to land transformation and hence a threat to the levels of biodiversity and ecosystem services (ES) vital to human endeavors and from which agriculture itself benefits. Growth in agriculture continues to accelerate, and it is estimated that agricultural lands could occupy an additional 200–300 million ha globally (mostly in Latin America and sub-Saharan Africa) in the next 40 y (1). With such mounting pressure and so much at stake, it is essential to find ways to meet agricultural demand while conserving critical ecosystems and minimizing overall impacts. In response, influential actors such as corporations and governments are creating policies, initiatives, agreements and the like that determine how and where agricultural development occurs. Typically, the objectives of these activities are based on reducing the relative and/or total impact of agriculture through avoidance of areas of High Conservation Value (2, 3) or High Carbon Stock (4).

Managing the demand for new agricultural land is undeniably important, and predictive modeling approaches for land development and management are urgently needed to better inform decision-making. Representation of the future for agriculture as a polarized choice between intensification and agricultural expansion is overly simplistic and unrealistic, especially given recent reports that yields of key commodities are saturating at levels far below that needed to meet increased demand (5). Future land development and management strategies will need to consider "land-sparing" approaches that consolidate and maximally intensify agriculture (6, 7) and "land-sharing" approaches that integrate natural and agricultural land into a more continuous mosaic (8, 9). It is likely that different strategies will work better in different places and at different scales, but questions about the optimal configuration and integration of agricultural and natural landscapes remain. To assess the impacts of future agricultural expansion at a landscape level, it is important to consider how and where such expansion may occur to understand resulting impacts on biodiversity and ES. Ecological theory suggests that the marginal value of the benefit provided by each unit of habitat conserved changes with the amount of total habitat area (10), and depending on the service, marginal values for the same type of habitat can vary widely based on its location relative to other habitat (11). Techniques for landscape optimization demonstrate the importance of where different land uses occur in determining the aggregate level of biodiversity or ES produced by a landscape (12).

Recent advances in scientific understanding and data availability have improved our ability to predict the impacts of land-use change on the levels of biodiversity and ES at the landscape level and have enabled the development of spatially explicit models of these ecosystem processes under different landscape configurations (13, 14). Tools to model the spatial variation in land-use change impacts on biodiversity and ES, including InVEST

Significance

Deforestation is a major threat to biodiversity and many ecosystem services and is closely linked to agricultural expansion. Sustainability assessment of different agricultural products and policies requires an understanding of the impacts of land conversion resulting from shifts in demand or incentives for production. The prevailing approaches to estimating such impacts do not account for the spatial context of the transformation. This study shows how different patterns of agricultural expansion into forested landscapes can vastly reduce or exacerbate the total impact, suggesting that methods to measure sustainability should consider not only the total area but also where and how the landscape is converted.

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[1]To whom correspondence should be addressed. Email: bchaplin@stanford.edu.

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(Integrated Valuation of Ecosystem Services and Trade-Offs) (15), GLOBIO (16), ARIES (17), and others, are now being used to help inform a wide range of decisions related to land-use planning, infrastructure investment, urban water supplies, and disaster risk reduction (18–21). In contrast to much of this site-based work often occurring in governmental decision contexts, considerations of biodiversity and ES by corporations and multilateral organizations typically rely on approaches that assign an amount of benefit or impact on a per-area basis, without representation of spatial variability (22). Global actors that indirectly or directly affect land use through sourcing decisions for commodity supply chains or investment decisions setting incentives for development would be better informed by approaches that could illustrate how their decisions play out across space.

In this paper we examine the impact of different spatial patterns of agricultural expansion on biodiversity (a metric of the average species response, mean species abundance) (*Methods*) and carbon storage (above-ground and below-ground biomass) to determine the degree to which the impacts of agricultural expansion can be reduced simply by influencing the pattern of land conversion. Many other ES, notably the provision of water, but also pollination and pest control, are vitally important to the continued productivity of agriculture. All of these services, as well as agricultural productivity itself, are variable in their production over space and their response to land-use change and are therefore important to consider in this way as well. We focus on carbon and biodiversity here as a first step because they feature prominently in existing sustainability assessments and are often considered solely on a per-area basis. Our goal is to highlight the importance of considering not only the total area of agricultural expansion, but also where the expansion occurs, differentiating between agricultural decisions that spread a small amount of impact over many places and those that consolidate a larger impact in fewer places. Field evidence shows lower biodiversity in small patches of forest and lower carbon stored in forest edges (see *Methods* for more detail). Translating such site-based information to broader assessment approaches is necessary to understand the potential importance of spatial configuration to land-use change impacts.

Study Regions in Brazil: Matto Grosso do Sul and Matto Grosso

Brazil is a microcosm of larger global trends in agricultural development and its resulting trade-offs. A biodiversity hotspot and one of the planet's largest stores of forest-based carbon, Brazil is also facing pressure for large-scale land transformation for agricultural production. It is the largest sugarcane producer and the second largest soybean producer in the world (23), and the area cultivated with these two crops has more than doubled in the past decade, with further increases predicted (24). The Brazilian government has established agro-ecological zoning plans for sugarcane (25), guiding the expansion of sugarcane in zones with underused and/or degraded pastures. There is no agro-ecological zoning in place for soy, but expansion of soy into the Amazon was restricted by a voluntary Soy Moratorium code until December 2014 (26). The regions of Mato Grosso do Sul and Mato Grosso were chosen for this study as these two states are particularly associated with Brazil's agricultural production and expansion plans. Mato Grosso do Sul is designated for future sugarcane expansion by the agro-ecological zoning plans, and Mato Grosso currently accounts for a third of soybean production in all of Brazil (27). For illustrative purposes, we allow agricultural production to expand into the Amazon in our simulations of expansion and habitat conversion, indicating the value of agro-ecological zoning or voluntary agreements such as the Soy Moratorium.

Simulating Agricultural Land Expansion in Landscapes

To test the sensitivity and to understand the value of a spatially explicit approach, we used a number of landscapes (real and theoretical) as well as different heuristic scenarios for agricultural land expansion. We plot the effects of agricultural expansion on biodiversity and carbon storage at small increments over a large range of land-use change for the following: (*i*) a theoretical landscape composed entirely of forest; (*ii*) baseline landscapes for the two study regions, modeled as a starting condition before human intervention; and (*iii*) actual landscapes for the two study regions determined by using 2012 vegetation cover (shown for a subregion of Mato Grosso, Fig. 1*A*). The first three scenarios simulate agricultural expansion into exclusively forest habitat: *edge* (Fig. 1*B*), which is from the forest edge in toward the cores of the forest areas; *core* (Fig. 1*C*), which is from the center of forest patches out toward the edges; and *fragmentation* (Fig. 1*D*), in which each step of agricultural expansion converts the forest pixels farthest from the forest edge. Although agricultural expansion likely involves many aspects of these examples, parsing them into separate scenarios allows us to examine the particular land-use patterns that may drive different responses, and it is useful for understanding the range of potential impacts. The fourth scenario, *current cropland* (Fig. 1*E*), simulates agriculture expanding out from current cropland into whichever habitats surround it.

These agricultural expansion scenarios are not intended to represent reality but rather to allow a better understanding of the mechanisms for different responses of biodiversity or an ecosystem service to agricultural expansion. The fragmentation scenario is more extreme than the typical branching patterns that occur when roads pierce forest interiors, but it provides an upper bound of impacts by reaching maximum fragmentation most efficiently. More complex land-use change modeling is necessary to inform real world decisions; however, this is a first step toward understanding the significance of different spatial patterns of land development. Exploring scenarios over these different types of landscapes demonstrates the effects of different spatial configurations of agricultural expansion and the role that the initial land-cover configuration plays in determining the nature of the response (*Methods* and *SI Appendix*).

Results

The spatial configuration of agricultural expansion can have dramatic impacts on the rate of loss of biodiversity and carbon storage because of patch size (lower species abundance in smaller patches) and edge effects (less carbon stored in forest edges). Conversion of forest to agriculture is most destructive when it occurs in a fragmentary pattern rather than in a consolidated patch. Fragmentation prompts a nonlinear response in both carbon and biodiversity for all landscape types, with the most damage occurring at the beginning of forest conversion (Fig. 2). Although the shapes and slopes of the responses of biodiversity and carbon storage to agricultural expansion are dependent on the initial configuration of the landscape, this effect of fragmentation is consistent in all but the most highly fragmented landscapes (Fig. 3).

Agricultural expansion is much more destructive to biodiversity, as measured by mean species abundance (MSA), when forest conversion occurs in the interior of habitat patches rather than along the forest edges. This effect is strongest in the theoretical forest landscape (Fig. 2, solid lines). In this hypothetical single patch of forest, conversion from forest edges has a negligible effect on MSA initially, whereas for both conversion of forest core and maximum fragmentation MSA deteriorates rapidly. There is a three- to fourfold difference in MSA between the forest edge and interior conversion scenarios at their widest spread for the same amount of total area converted. At 40% of the theoretical forest converted, fragmentation and forest core conversion reduce MSA

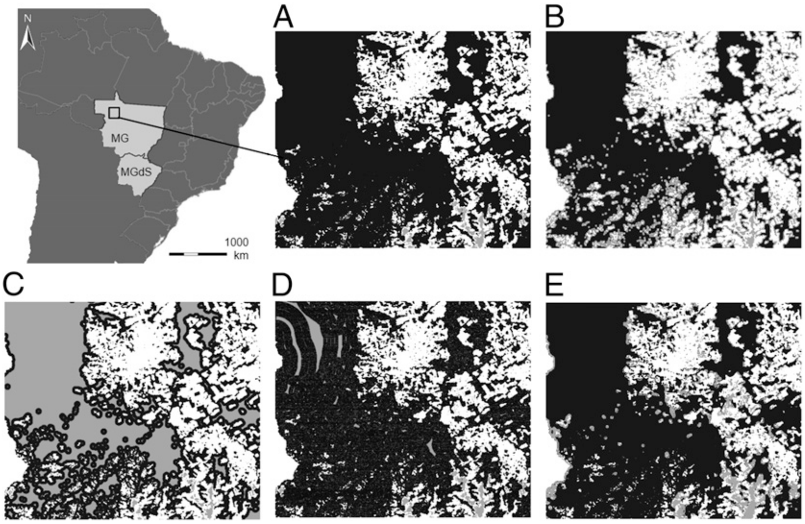

Fig. 1. Scenarios for agricultural expansion with forest in black, agriculture in gray, and all other habitat in white. A sample subregion [shown as the square frame in the *Inset* map of Mato Grosso (MG) and Mato Grosso do Sul (MGdS) Brazil] is magnified to show its current condition before agricultural expansion occurs (*A*). A snapshot of agricultural expansion at 40% of total forest conversion (equivalent to 200–400% production increase of soy) illustrates the different spatial patterns of the expansion scenarios: (*B*) *edge*: from forest edge in; (*C*) *core*: from forest core out; (*D*) *fragmentation*: maximally fragmenting the landscape; and (*E*) conversion into whichever habitats surround *current cropland*. Note that although these snapshots contain the same amount of converted land, the region shown has been magnified to highlight the visual differences that are more difficult to see at the full extent. Thus, the magnified version shows a large amount of conversion in the heart of a thick forest in the core scenario, but relatively little land converted in the edge scenario because the converted land is distributed around all of the forest edges throughout the whole region, the full extent of which is not shown.

by 70–80% whereas forest edge conversion loses only 10% of original MSA.

Unlike biodiversity, carbon storage does not have a markedly different response to forest conversion from the edge in versus the core out, even in the theoretical forest landscape (Fig. 2, dashed lines). However, fragmentation has a very strong effect on carbon in the early stages of forest conversion, cutting carbon storage values in half when as little as 10% of the theoretical forest is converted. Compared with the few percent of carbon storage loss in the forest edge and core scenarios at the same level of conversion, these impacts of fragmentation are an order of magnitude higher than more consolidated agricultural expansion.

The difference between the forest edge and core conversion scenarios is not as pronounced in real landscapes that are more heterogeneous and patchy, but fragmentation remains substantially worse than all other scenarios. For Mato Grosso's baseline (pre-human) landscape, fragmentation is more than twice as damaging to MSA as other forms of forest conversion at the widest spread between scenarios (26 million ha converted; Fig. 3*A*, solid lines) and similarly to carbon (at 8 million ha converted; Fig. 3*A*, dashed lines). Absolute impacts of agricultural expansion are subtler for the patchier forest in the baseline landscape of Mato Grosso do Sul (Fig. 3*B*); this is partly because the starting values for MSA and carbon are lower in these landscapes, so there is less to lose. However, fragmentation still reduces both MSA and carbon by more than twice the level of the other scenarios at the widest spread between them.

Remarkably, the forest core and edge scenarios in the actual landscapes follow a similar pattern as the baseline simulation for both MSA and carbon in Mato Grosso, despite the fact that they are starting from very different reference points (with the baseline landscapes containing far more forest than currently exists in the actual landscapes) (*Methods* and *SI Appendix*). The fragmentation scenario is still nearly twice as damaging to MSA and carbon storage as the other forest conversion scenarios in Mato Grosso (Fig. 3*C*) at the widest spread between scenarios, by around 11 million ha converted for biodiversity and 7.1 million for carbon (corresponding to a 170–340% and 100–200% increase in soy production, respectively, depending on double cropping). In fact, the difference between forest edge conversion and fragmentation is nearly as great as the difference between forest edge conversion and expanding out from current cropland, despite a much lower total amount of forest converted in the latter (only 20% of total current forest area in Mato Grosso and 10% in Mato Grosso do Sul) (*SI Appendix*). This highlights the importance of considering forest habitats as unequal in their provision of biodiversity and ES across space. Differences between scenarios are much more muted in the actual vegetation landscape of Mato Grosso do Sul (Fig. 3*D*), where the only pronounced difference is between the forest conversion scenarios and the current cropland scenario. The forest in this region is already highly fragmented (with only 6% of the total area in forest, accounting for only 20% of baseline forest

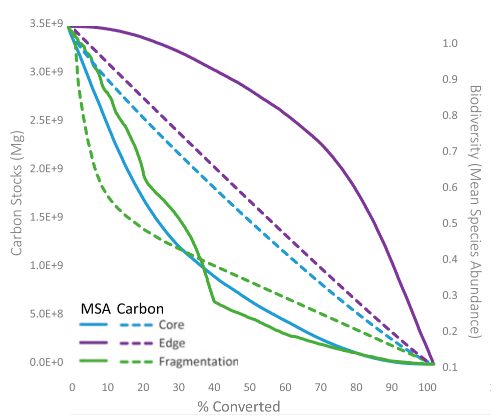

Fig. 2. Impacts of agricultural expansion simulated in a theoretical landscape (one single continuous patch of forest). Change in carbon stocks [Mg (megagrams) on left axis] and biodiversity ("mean species abundance" on right axis) is shown for agricultural expansion into forest *core* (blue), forest *edge* (purple), or forest with maximum *fragmentation* (green). Solid lines show response of MSA, and dashed lines represent carbon.

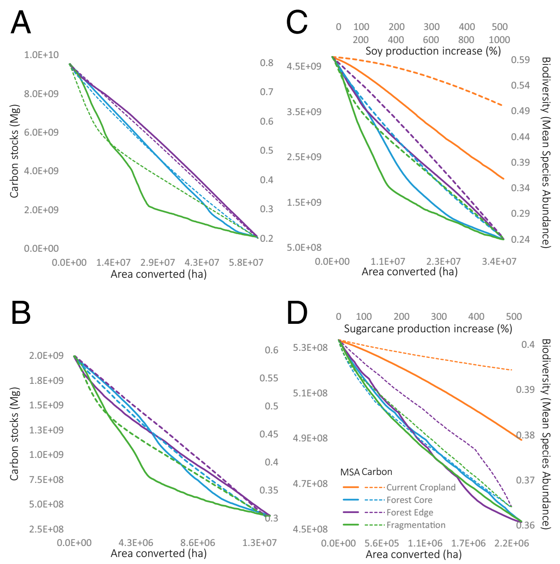

Fig. 3. Impacts of agricultural expansion in baseline landscapes (unmodified by human activity, but with multiple patches of different types of natural habitat, according to a potential vegetation map) for Mato Grosso (*A*), Mato Grosso do Sul (*B*), and in actual landscapes (vegetation from current land-cover map) for Mato Grosso (*C*) and Mato Grosso do Sul (*D*). As in Fig. 2, change in carbon stocks (Mg on left axis; dashed lines) and biodiversity ("mean species abundance" on right axis; solid lines) are shown for *core* (blue), *edge* (purple), and *fragmentation* (green) scenarios, and for actual landscapes only, expansion from *current cropland* (orange). Confidence intervals for each scenario can be seen in *SI Appendix*.

area) (*SI Appendix*), which may already be too diffuse to be substantially impacted by further fragmentation.

Discussion

In the context of understanding the consequences of different patterns of agricultural expansion, the dramatic impact of fragmentation is striking. Expansion of agriculture into the nearest neighboring lands rather than fragmenting forest reduces impacts by more than three times for biodiversity or an order of magnitude for carbon storage for the same increase in agricultural area. However, even something as simple as gradually spreading into a forest as opposed to jumping ahead beyond the current forest edge can cut the losses to carbon or biodiversity in half for the same amount of forest converted. This means that policies that encourage expansion around existing agriculture or edges of forests, as opposed to large infrastructure efforts such as roads that leapfrog agricultural development into frontier habitats, may lead to disproportionately lower impacts for biodiversity and carbon.

One caveat to this conclusion is that "fragmentation," as simulated in this study, does not realistically depict the fragmentation that occurs following road development, which typically shows a feather or spoke-like pattern of development radiating from roads. The speckled fragmentation pattern formed by agriculture within our fragmentation scenario maximizes the number of forest edges, but does not truly isolate patches until a large portion of the forest has already been converted. This explains why this scenario is more destructive to carbon stocks than to biodiversity. The fact that similar trends are seen in both the multiple-patch heterogeneous baseline landscapes and in the homogenous single-forest patch theoretical landscape shows that the effect of fragmentation operates almost independently of forest patch size for both biodiversity and carbon. Even the substantially patchier forest extent in the actual landscape of Mato Grosso conforms to this general relationship; only the highly fragmented actual forest of Mato Grosso do Sul fails to show such a response. Although more erratic patterns formed by real fragmentation forces, such as roads, may not be as efficient at creating forest edges, the extreme sensitivity of the response of both carbon and biodiversity to this scenario suggests that any fragmentation rather than consolidated expansion is likely to have a nonlinear effect on carbon and biodiversity.

The shape of the responses of biodiversity or carbon storage could be framed in terms of land-sharing vs. land-sparing from the perspective of the number of patches of agriculture rather than the typical focus on total area affected. A concave relationship, initially flat and steepening with increasing habitat loss (such as for MSA with forest conversion from the edge in the theoretical landscape), would suggest that a certain amount of expansion could occur with little impact, and in such a case a land-sharing approach would be preferable. In contrast, a convex relationship, steepest initially and flattening out with increasing habitat loss (such as for the forest core or fragmentation scenario), would suggest that the greatest impact would occur right away, in which case consolidating agricultural expansion into as few different places as possible would help to minimize the impact on biodiversity. It has been noted that the empirical data required to test hypotheses about the extent to which we should separate or integrate agriculture and conservation are scarce (28) and the difference between the two may ultimately be a question of scale, with land-sparing at the field level becoming land-sharing in a mosaic at the landscape level (29). Analyses such as this, if combined with spatially explicit information about yields, can help test hypotheses about the most beneficial scale of agricultural consolidation.

Although it is generally only biodiversity that is considered in the land-sharing/land-sparing debate, Balmford et al. (30) do point out that investment in agricultural intensification can deliver cost-effective climate mitigation through land-sparing measures that prevent carbon emissions from deforestation. Considering land-sparing again from the frame of number of places, not just total area, could also benefit carbon storage because there is a convex relationship between forest-edge creation and carbon-storage decline. Carbon emissions could be minimized by avoiding forest-edge creation through the consolidation of agriculture into fewer places. Comparison of current hotspots of biodiversity and carbon storage highlights the importance of considering these two objectives together because, although synergies can be found, they are not guaranteed by managing for one and not the other (31). Mapping at the global scale has shown that biodiversity and ES are not spatially correlated, but there are places where win–wins can be achieved (32). In our simulations, the most damaging effects of fragmentation level off (or the relationship with agricultural expansion becomes less steep) earlier for carbon than for biodiversity. These specific results depend heavily on the assumptions of our models and land-use change simulations, but continuing to refine this approach will enable such comparisons of different conservation objectives.

Biodiversity and carbon are just two considerations in a multitude of benefits and trade-offs that must be weighed when evaluating the change resulting from agricultural expansion. Wild-food provisioning, pest control, pollination, water regulation, flood protection, and microclimate regulation (e.g., wind, humidity) are all among the ES provided by forest or other natural habitats, and they may all provide substantial value to agriculture when colocated. As the modeling of these other ES advances, they should be included in land-sharing/land-sparing or agricultural configuration analyses such as those described here to understand the full pace and magnitude of agricultural impacts and to guide future agriculture into safer places for expansion. These spatially explicit analyses could be further improved by considering spatial differences in agricultural productivity, reducing the total area needed for expansion by optimizing yields in concert with other ES (12). Indeed, analyzing biodiversity and ES alongside the value and profitability of food production is imperative if we are to fully understand the implications of land-use decisions (33).

It is of critical importance to integrate this type of spatially explicit ES science into mainstream impact assessment approaches. Many corporations use Life Cycle Assessment to estimate potential environmental impacts (including those from land-use change) of product systems (34). This approach is now finding use beyond the corporate sector to analyze sustainability at consumer and country levels (35), and accounting frameworks throughout the sustainability community use similar approaches such as carbon or water foot-printing (36). The methods for assessing land-use impacts in these approaches typically rely on weighted averages that aggregate data for different climate regions, biomes, and soil types (34, 37) but fail to account for the spatial dependency of biodiversity or ecosystem processes shown here to depend so heavily on landscape configuration and patterns of land-use change. If spatial context changes the effective rate of loss of biodiversity or an ecosystem service with area of habitat lost, nonspatial accounting of land-use change impacts could prove drastically inaccurate.

Although the use of spatially explicit information about changes to biodiversity and ecosystem services would lead to better assessments of land-use impacts than the current standard, some complexities not represented here may further affect results and deserve attention. The strength of fragmentation effects on biodiversity has been studied extensively, but often has not been adequately separated from the effects of change in total habitat area (38). The GLOBIO approach used here does treat fragmentation and habitat area independently, but the relationship between the two are not fully understood, and the degree to which fragmentation can affect the amount of habitat required for species persistence varies widely depending on the processes considered (with colonization–extinction models predicting much more dramatic effects of fragmentation than birth–immigration–death–emigration models) (39). In contrast to biodiversity, our understanding of the effects of fragmentation on carbon storage is more preliminary and should be extended to more geographies and climates to establish a more generalized relationship. Furthermore, both of these models assume a static state of habitat outside of the direct land-use changes considered in the scenarios, whereas in reality large-scale landscape transitions may affect microclimate or other factors that determine ecosystem structure and function; the incorporation of ecological thresholds and state-changes into land-use changes and ecosystem service modeling remains a critical frontier for further research (40).

Despite its simplicity, we believe this approach is a fundamental step toward predicting the nature of ecological response to agricultural or wider land-use expansion. The range of scenarios tested here provides a sense of the importance of understanding the specific details of land-use change in a particular region. It is unrealistic to expect nations or regions to curtail agricultural expansion when there are such pressing needs for food or income. However, it is feasible to imagine best management practices and zoning approaches that promote one spatial pattern of agricultural lands over another. Development of such policy mechanisms will obviously need to take into account other rural development objectives such as poverty alleviation, job creation, and economic stability, but better information on the maintenance and delivery of ES under different patterns of land-use change is essential to anticipating the outcomes of different policies and decisions. Spatially explicit methods could feed into corporate decisions on commodity sourcing at different scales (countries, states within countries, and more localized landscapes), helping to identify possibilities for impact reduction based on agricultural placement, as well as mitigation options at other stages of product value chains. At the same time, such methods could aid policy decisions on zoning agricultural expansion or agricultural development projects through moratoriums, legislation, land tenure reform, financial incentives, or other mechanisms. Smarter planning and strategy taking spatial context into account can allow us to meet development and growth targets while maintaining our most vital and sensitive resources and life-support systems.

Methods

Agricultural Expansion. We consider a full conversion of all forest in the landscape to provide a context for the total magnitude and rate of change in biodiversity and carbon storage over the entire range of forest extents. The three full-forest conversion scenarios (core, edge, fragmentation; Fig. 1 *B–D*) are simulated in the theoretical, baseline, and actual landscapes described below. The current cropland scenario (Fig. 1*E*) is simulated only in the actual landscape because there is no cropland from which to expand in the theoretical or baseline landscapes.

Theoretical Landscape. The theoretical landscape is a computer-generated matrix composed entirely of forest as its starting condition, simulating one large continuous homogeneous patch of forest. This demonstrates the effects of different patterns of fragmentation on biodiversity and carbon storage without additional complexities introduced by existing landscape heterogeneity or patch dynamics before the simulation begins.

Baseline Landscape. Whereas the theoretical landscape starts from an entirely forested area, the baseline and actual landscapes are grounded in the more realistic context of the Mato Grosso and Mato Grosso do Sul states of Brazil. The baseline landscape is initially composed only of the natural ecosystems (e.g., forest, savanna, and grassland) assumed to be present before human intervention (41). It provides a reference state from which the full effect of forest conversion can be compared with both the actual landscape and the theoretical landscape.

Actual Landscape. The actual landscapes of Mato Grosso and Mato Grosso do Sul are derived from 2012 land cover in 14 classes mapped by MODIS (Moderate Resolution Imaging Spectroradiometer). Simulating agricultural expansion in the actual landscapes allows for an exploration of the effects of forest conversion from an already partially fragmented starting condition, which may mute further fragmentation effects. The resulting shape and slope of the ecosystem responses to agricultural expansion in this landscape can thus be compared with the responses in a more natural but still heterogeneous landscape (given by the baseline landscape) and to the general shape of the relationship (given by the theoretical landscape).

The initial configurations of the landscapes examined here differ quite widely, with the baseline landscapes containing nearly twice the amount of forest as the actual landscape for Mato Grosso and more than five times that for Mato Grosso do Sul (62 ha compared with 35 million ha in Mato Grosso; 13 ha compared with 2.2 million ha in Mato Grosso do Sul) (*SI Appendix*). If the baselines are accurate, this means that half the forest in Mato Grosso and the vast majority of the forest in Mato Grosso do Sul have already been converted. The conversion to agriculture of all remaining forest in these states corresponds to a 500% increase in the current production of sugarcane in Mato Grosso do Sul and a 500–1,000% increase in current production of soy (depending on assumptions about double cropping) in Mato Grosso, based on current yield data (42) and assuming no gains from intensification. Although the full conversion of all remaining forest is highly unlikely in any region, it provides a way of comparing the shape of response across regions and different landscapes, and any point of production increase along the way can be considered for impacts of different agricultural expansion patterns.

Ecological Response. We adapted and applied models for biodiversity (GLOBIO) and carbon storage (InVEST) to assess ecosystem response to incremental changes in land use according to the progressive agricultural expansion scenarios. These models calculate the biodiversity or ES produced in different habitats and resulting from a change in the structure of ecosystems.

The GLOBIO model (16) predicts MSA in response to land-use, fragmentation, infrastructure, climate change, and pollution threats through a meta-analysis of the impact of each of these threats on individual species abundances. Each threat provides a weight that diminishes the level of MSA relative to "pristine" conditions, and the weights are multiplied together to produce an overall index of change in MSA in response to change in threats. MSA does not correspond directly to species richness, evenness, or other common metrics of biodiversity. Depending on the distribution of abundances of different species in a community, a given decline in MSA could be associated with different magnitudes of declines in species richness. The modeled decline of global MSA from a pristine or prehuman state falls within the range of more rigorously modeled bird abundance declines (16, 43). However, the decline in MSA by 2050 estimated by GLOBIO is lower than the loss of vascular plant diversity projected by the Millennium Ecosystem Assessment (16), and comparisons to direct observations via the Living Plant Index have confirmed this tendency of MSA to underestimate losses (44). Therefore, the response of species richness to the agricultural expansion scenarios investigated here may be even more dramatic than that of MSA.

The InVEST carbon model (15) uses an inventory approach to project changes in carbon storage resulting from land-use change, as applied by global mapping efforts used widely in carbon accounting (45), following guidance by the Intergovernmental Panel on Climate Change (IPCC) (46, 47). In this approach, above- and below-ground carbon storage values are assigned to different habitat types based on IPCC Tier 1 data or more regionally specific literature review where possible and multiplied by the area of each habitat type to derive the total carbon stored in a region. Although accurately capturing average values, this approach does not represent variability within specific habitat types, which is of concern when considering changes in habitat configuration.

To explore differences between alternate scenarios of agricultural expansion, it is important to represent possible fragmentation and edge effects that make the value of 1 ha of forest in one location different from 1 ha of forest in another location. We include several adaptations to better capture this spatial variability in our modeling of biodiversity and carbon responses to incremental land-use change. First, we are able to apply GLOBIO at a fine resolution with globally available data by improving the designation of different land-use types (e.g., managed pasture vs. grassland, managed vs. primary-growth forest), and we develop a method for estimating fragmentation using a Gaussian filter to smooth individual pixel changes. Second, we adapt the InVEST carbon model to account for empirical evidence that higher mortality rates for large trees exist in forest edges, and thus the amount of carbon that vegetation can store increases with distance from forest edge (48, 49). We use the pantropical carbon and associated land cover datasets created by the Woods Hole Research Center (50) to construct a logarithmic regression between distance to forest edge and forest biomass and apply that predictive relationship to all forest pixels in our scenarios. Above-ground carbon estimates for nonforest habitat and below-ground carbon estimates for all habitats were taken from the literature (soil carbon was not considered in this analysis). Additional details of these methods can be found in the *SI Appendix*.

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