Biological Conservation 204 (2016) 221–230

Contents lists available at ScienceDirect

Biological Conservation

journal homepage: www.elsevier.com/locate/bioc

Optimizing land use decision-making to sustain Brazilian agricultural profits, biodiversity and ecosystem services

Christina M. Kennedy [a,*], Peter L. Hawthorne [b,*], Daniela A. Miteva [c], Leandro Baumgarten [d], Kei Sochi [a], Marcelo Matsumoto [d], Jeffrey S. Evans [a], Stephen Polasky [b,e], Perrine Hamel [f], Emerson M. Vieira [g], Pedro Ferreira Develey [h], Cagan H. Sekercioglu [i,j], Ana D. Davidson [k], Elizabeth M. Uhlhorn [l], Joseph Kiesecker [a]

[a] Global Conservation Lands Program, The Nature Conservancy, Fort Collins, CO 80524, USA
[b] Natural Capital Project & Institute on the Environment, University of Minnesota, 325 Learning & Environmental Sciences, 1954 Buford Ave, St. Paul, MN 55108, USA
[c] Department of Agricultural, Environmental, and Development Economics, The Ohio State University, Columbus, OH 43210, USA
[d] Brazil Program, The Nature Conservancy, SIG Qd. 01, Lt. 985-1005, Sala 206, Brasília/DF 70610-410, Brazil
[e] Department of Applied Economics, University of Minnesota, 1994 Buford Ave, St. Paul, MN 55112, USA
[f] Natural Capital Project, 371 Serra Mall, Stanford University, Stanford, CA 94305, USA
[g] Laboratório de Ecologia de Vertebrados, Departamento de Ecologia, C.P. 04457, Universidade de Brasília, Campus Universitário Darcy Ribeiro, Brasília, Distrito Federal 70910-900, Brazil
[h] BirdLife/SAVE Brasil, R. Fernão Dias 219, cj.2, São Paulo, SP 05427-010, Brazil
[i] Department of Biology, University of Utah, Salt Lake City, UT, 84112, USA
[j] College of Sciences, Koç University, Rumelifeneri, Sariyer, 34450, Istanbul, Turkey
[k] Department of Ecology and Evolution, Stony Brook University, Stony Brook, NY 11794-5245, USA
[l] The Dow Chemical Company, Sustainability Program, Philadelphia, PA 19106, USA

ARTICLE INFO

Article history:
Received 23 March 2016
Received in revised form 15 September 2016
Accepted 24 October 2016
Available online 31 October 2016

Keywords:
Sustainable agriculture
Production possibility frontier
Land use optimization
Land use policy
Tropical conservation

ABSTRACT

Designing landscapes that can meet human needs, while maintaining functioning ecosystems, is essential for long-term sustainability. To achieve this goal, we must better understand the trade-offs and thresholds in the provision of ecosystem services and economic returns. To this end, we integrate spatially explicit economic and biophysical models to jointly optimize agricultural profit (sugarcane production and cattle ranching), biodiversity (bird and mammal species), and freshwater quality (nitrogen, phosphorus, and sediment retention) in the Brazilian Cerrado. We generate efficiency frontiers to evaluate the economic and environmental trade-offs and map efficient combinations of agricultural land and natural habitat under varying service importance. To assess the potential impact of the Brazilian Forest Code (FC), a federal policy that aims to promote biodiversity and ecosystem services on private lands, we compare the frontiers with optimizations that mimic the habitat requirements in the region. We find significant opportunities to improve both economic and environmental outcomes relative to the current landscape. Substantial trade-offs between biodiversity and water quality exist when land use planning targets a single service, but these trade-offs can be minimized through multi-objective planning. We also detect non-linear profit-ecosystem services relationships that result in land use thresholds that coincide with the FC requirements. Further, we demonstrate that landscape-level planning can greatly improve the performance of the FC relative to traditional farm-level planning. These findings suggest that through joint planning for economic and environmental goals at a landscape-scale, Brazil's agricultural sector can expand production and meet regulatory requirements, while maintaining biodiversity and ecosystem service provision.

© 2016 The Authors. Published by Elsevier Ltd. This is an open access article under the CC BY-NC-ND license (http://creativecommons.org/licenses/by-nc-nd/4.0/).

1. Introduction

An additional 1 billion ha of agricultural land are predicted to be necessary to meet future demands for food, fiber, and fuel (Tilman et al., 2011). Much of this expansion in cropland and pastureland is taking place in forest-rich tropical regions: >80% of new agricultural land between 1980 and 2000 came at the expense of tropical forests (Gibbs et al., 2010); over 34% of recent global tropical deforestation (2000–2012) occurred in Brazil (Hansen et al., 2013). Agricultural expansion in tropical regions negatively impacts natural habitats and the ecosystem services they provide: e.g., regulating and purifying water (Power, 2010), regulating climate through carbon storage (Baccini et al., 2012), and supporting the majority of the world's biodiversity (Jenkins et al., 2013). On the other hand, agricultural expansion is important to food security and economic development (Ramankutty et al., 2008). As a result, planning strategies are needed that can increase

* Corresponding authors.
E-mail addresses: ckennedy@tnc.org (C.M. Kennedy), phawthorne@umn.edu (P.L. Hawthorne).

http://dx.doi.org/10.1016/j.biocon.2016.10.039
0006-3207/© 2016 The Authors. Published by Elsevier Ltd. This is an open access article under the CC BY-NC-ND license (http://creativecommons.org/licenses/by-nc-nd/4.0/).

agricultural production while sustaining local biodiversity and ecosystem services provision.

Previous studies have tackled this challenge by spatially mapping ecosystem services under alternative land use scenarios (e.g., Bateman et al., 2013; Koh and Ghazoul, 2010; Law et al., 2015; Nelson et al., 2009; Qiu and Turner, 2013). Importantly, their findings reveal that landscapes that maximize only commodity production provide smaller net social and environmental benefits than landscapes that also prioritize other ecosystem services (e.g., water quality, carbon sequestration). Further, they demonstrate that it is possible to provide high levels of multiple services by considering land-use trade-offs and carefully targeting the allocation of land use activities across a region. The majority of research, however, tends to be limited by considering only current landscape conditions or a few pre-selected scenarios, and by evaluating outcomes based on a limited range of values ascribed to different services. As such, potential thresholds in ecosystem service provision or the most efficient land-use options for multiple services may go undetected. Expanding upon existing work, we model a range of land-use scenarios and map efficient combinations of agricultural land and natural habitat across varying levels of agricultural production (expansion) under different service values. We apply this approach to a watershed in the Brazilian Cerrado to inform landscape design that can sustain economic activities together with biodiversity and ecosystem services in the face of agricultural expansion.

1.1. Case study in the Brazilian Cerrado

The Cerrado biome harbors some of the highest levels of species richness and endemism in the world, but has lost more than half of its original extent due to cattle ranching and expansion of cash crops, such as sugarcane and soybeans (Klink and Machado, 2005). With absolute deforestation rates in the Cerrado now surpassing those in the Amazon (Soares-Filho et al., 2014) and with habitat loss projected to continue (Lapola et al., 2010), the remaining natural vegetation and ecosystem services that they support are at risk (Klink and Machado, 2005). Thus, strategic land-use planning is needed to support livelihoods while also protecting unique habitats for biodiversity and providing clean surface water.

Current land use planning in the region is governed by Brazil's Forest Code (FC): a federal policy that targets the protection of biodiversity and hydrological services by mandating that a portion of natural vegetation be maintained on private lands (Soares-Filho et al., 2014). Farm-by-farm planning is required for FC compliance (Soares-Filho et al., 2014; Sparovek et al., 2012a), but planning at a larger (e.g., watershed) scale may better capture economies of scale for both agricultural production and ecosystem services provision (Swift et al., 2004), and thereby improve the impact of the FC (Kennedy et al., 2016). Brazilian states and licensing agencies can influence the location of protected and restored habitats and promote landscape planning, for example, by requiring consideration of habitat connectivity in the placement of required natural vegetation (Silva et al., 2012). To assess the potential benefit of such larger-scale FC compliance, we model the outcomes for agricultural production and environmental quality in a Cerrado watershed at two scales, property (farm)-level (PL) and landscape-level (LL).

1.2. Multi-service spatial optimization

We apply a spatial optimization approach to examine the trade-offs and thresholds in the provision of agricultural profit (AP) and ecosystem services (ES), proxied by freshwater quality (WQ) and biodiversity (BD). For brevity, we collectively refer to BD and WQ as ES. Although food production is an ES by many classification schemes, we distinguish AP from BD and WQ in our assessment to evaluate the trade-offs between marketed and non-marketed services (given that the former are often produced at the expense of the latter) (Carpenter et al., 2009).

We integrate detailed spatially explicit models of AP (cattle ranching and sugarcane production), BD (number of bird and mammal species) and WQ (nitrogen, phosphorus, and sediment retention) to construct efficiency (or production possibility) frontiers (Figs. 1, 3) (*sensu* Polasky et al., 2008) that map efficient combinations of agricultural land and natural habitat, so that no increase in a service is possible without decreasing another. We generate separate frontiers for each of the combinations between AP and the ES, using a range of weights (as described below). Varying the weights placed on BD and WQ allows us to evaluate a range of predicted landscape outcomes under different service preferences without imposing any assumed social value. To compare the effects of planning at different scales, we generate efficiency frontiers 1) with no restriction on the amount or location of habitat or agriculture (referred to as "unconstrained"); 2) enforcing a 25% habitat constraint on each farm (referred to as "property-level" or PL, mimicking the Forest Code); and 3) enforcing a 25% habitat constraint across the entire landscape (referred to as "landscape-level" or LL, the whole-landscape comparison to FC) (see Table 1).

Our approach is a methodological advance from previous ES optimizations, which have been based on simplified or artificial landscapes at small spatial scales (e.g., 1 km^2) (e.g., Cong et al., 2016; Groot et al., 2007) or have targeted only BD (e.g., Polasky et al., 2008) or a single service like pollination (e.g., Brosi et al., 2008) or timber production (e.g., Lichtenstein and Montgomery, 2003), but have not considered more than two ES objectives. We build upon these efforts by optimizing land uses for multiple ES across an entire watershed and accounting for the spatial dependencies of ES dynamically in land cover optimizations. Further, we vary the importance for BD and WQ to assess their trade-offs at a watershed-scale, and vary the planning scale (PL vs. LL) to evaluate the benefits of spatial coordination of land use. Our aim is to demonstrate the theoretical potential of land-use planning approaches under varying service preferences at different planning scales to improve agricultural production and to sustain multiple ecosystem services.

In contrast to the more commonly applied scenario-based assessments (e.g., Bateman et al., 2013; Koh and Ghazoul, 2010; Law et al., 2015; Nelson et al., 2009; Qiu and Turner, 2013), the efficiency frontiers allow us to (1) assess whether current land use planning and policies like the Forest Code are efficient or whether improvements can be made to increase both agricultural production and ecosystem service provision, (2) examine the inherent complementarities and trade-offs between the environmental and economic objectives, and (3) identify potential thresholds in ES provision along a continuum of possible efficient combinations of land use. Thus, this approach has significant implications for improving agricultural and conservation policies in hotspots like the Brazilian Cerrado.

2. Methods

2.1. Study area and Forest Code requirements

Our study area encompasses the ~400,000 ha Ribeirão São Jerônimo watershed in Brazil's southeastern agricultural region (Fig. S1). It is currently comprised of mainly pasture that is being converted to sugarcane (Klink and Machado, 2005; Lapola et al., 2010). <20% of the natural habitat remains, made up of four dominant vegetation types (cerrado, cerradão, semi-deciduous forests, and wetlands) (Fig. S2, Table S1). All remnant natural vegetation is on private lands and is regulated by the FC. In our region, this law requires that each farm maintains ~25% of its area in natural vegetation. This percentage is based on our assessment of the FC requirements using publicly available farm boundary maps combined with field surveys. For the PL scenarios, 25% of a farm's area is placed under natural vegetation; for the LL scenarios, 25% of the total area of the watershed, regardless of land tenure, is allocated across the watershed. This percentage requirement is composed of both 1) Legal Reserves (LRs), which require ~20% natural area set-asides

Table 1
Summary of the efficiency frontiers constructed that depict the trade-offs between agricultural profit and an ecosystem service objective (calculated as a weighted sum of biodiversity (BD) and water quality (WQ)). The frontiers differ in the preference (weight) for BD and WQ for each profit level and in the planning scale related to compliance with the Brazilian Forest Code (FC). In our study region, the FC requires that each farm maintains ~25% of its land area in natural vegetation, which was met per farm at the property scale and for the entire watershed at the landscape scale (for more details see SI text S§1.1). For all frontiers, we generated tradeoffs when land use was optimized for profit versus only BD or only WQ, and jointly for BD and WQ to achieve intermediate outcomes. See Fig. 1 for unconstrained frontiers and Fig. 3 for the property-and landscape-level frontiers.

Planning scale	Name	%Natural habitat restriction	Ecosystem services objective
Unconstrained	Only BD	None	High BD only
Unconstrained	High BD	None	High BD + low WQ
Unconstrained	Medium BD	None	Medium BD + medium WQ
Unconstrained	Low BD	None	Low BD + high WQ
Unconstrained	Only WQ	None	High WQ only
Landscape-level	Only BD	25% for the watershed	High BD only
Landscape-level	Medium BD	25% for the watershed	Medium BD + medium WQ
Landscape-level	Only WQ	25% for the watershed	High WQ only
Property-level	Only BD	25% per farm	High BD only
Property-level	Medium BD	25% per farm	Medium BD + medium WQ
Property-level	Only WQ	25% per farm	High WQ only

anywhere on farms to protect biodiversity as required in the Cerrado biome, and 2) Permanent Protected Areas (PPAs), which require ~5% of vegetation be placed along stream banks and steep slopes to protect water quality. Given the resolution of our data (90 m pixels), we do not model the exact location of PPAs legally required along riparian areas (width varies between 5 and 30 m depending on the farm size). Instead, we allow PPAs along with LRs to be placed according to our spatial optimization models to evaluate the impacts of different spatial configurations based on different service preferences (see below). Thus, our results should not be strictly interpreted as specific, legally permissible land use options. Rather our approach captures the intent of the FC, while being generalizable to other regions and legal or planning contexts. See SI S§1.1 for details on the study area, land tenure mapping, and Forest Code requirements in the region.

Supplementary material to this article can be found online at http://dx.doi.org/10.1016/j.biocon.2016.10.039.

Other Supplementary data for this manuscript is provided on Conservation Gateway at: http://nature.org/TNC-Dow-Brazil.

2.2. Agricultural profit modeling

Our models target the two main agricultural activities in the region: cattle ranching and sugarcane production. Although other agricultural land uses exist (row crops and plantations), they were not included in the models because they make up <1% of land area (Kennedy et al., 2014) and, in contrast to sugarcane production, are not targeted for commercial expansion in the region (Dow Chemical, 2008).[1] In our models, all land in the study watershed, with the exception of water bodies and infrastructure, can be converted to either sugarcane or pastures; an assumption that is tenable for the region. For each agricultural activity, we constructed spatially explicit profit models based on the differences between the annual revenue and the annual production costs using exceptionally detailed data obtained from a local commercial sugarcane producer (S§1.2a) and net profits from cattle ranching studies from the area (S§1.2b). The sugarcane yield model predictions were verified with actual yields from nearby locations; the sugarcane and cattle ranching profits were consistent with other studies. Our profit models are static and deterministic and do not model the processes underlying the spatial patterns of development (e.g., placement of mills, roads, or houses). See SI S§1.2 for details and S§3 for modeling caveats.

[1] We note that while we do not model other crops (e.g., soybeans), the same approach could be taken to do so.

2.3. Biodiversity and water quality modeling

We modeled 407 terrestrial bird and 132 mammal species expected to occur in the study region (Table S2) using the Polasky et al. (2008) model. This model predicts species-specific persistence probabilities based on: 1) the amount of habitat required for a breeding pair, 2) the relative suitability of habitat types, and 3) the ability of species to disperse among patches in the landscape. These variables were parameterized based on species information from global databases and field guides and determined based on allometric relationships for body size, trophic guild, and home range size (Tables S3–S4). We also assessed species compositional shifts in relation to the following ecological and life history traits: trophic level, body size, habitat association, habitat breadth, diet guild, diet breadth, endemism, conservation status, and migratory status. See S§1.4 for details.

To quantify WQ services, we used the terrestrial nutrient and sediment models from InVEST 2.5.6 (Tallis et al., 2013). These models predict the amounts of N, P, and S in surface waterways for a given land use pattern based on slope, soil characteristics, vegetation types, land management, export and retention coefficients. We parameterized the models using local studies and spatially explicit data (SI S§1.3). To generate the frontiers, we converted the absolute N, P, and S loads for each landscape to a reduction from a landscape that has only agriculture and no natural vegetation. In the optimization, N and S were normalized into a single weighted WQ index; P was dropped due to its high correlation with S.

The BD and WQ models were based on steady-state systems and were parameterized using spatially explicit data and parameters from studies in the biome whenever available. Predictions from our biophysical models were consistent with published studies in the Cerrado or deemed reasonable by expert review when studies were not available. See SI for further details.

2.4. Land use optimization

We combined the AP, BD, and WQ models with optimization techniques and constructed efficiency frontiers that depict the trade-offs between AP and an ES objective (calculated as a weighted sum of BD and WQ). One of the main challenges of optimizing ES is that, in many cases, the value of a single land-unit for ES provision depends non-linearly on the land use in neighboring units. To address the spatial dependence issue, we used a greedy algorithm that updates the marginal value of each potential land-use change per iteration. That is, the optimization procedure allocated land use on the basis of its relative suitability for agricultural profit for sugarcane and cattle ranching, bird and mammal species richness, and N and S retention using iterated local search algorithms. This approach builds on that of Polasky et al. (2008) and accounts for profit-conservation trade-offs not only in terms of species habitat but also water purification.

Each optimization generated an allocation of three land uses - cattle ranching, sugarcane production, and natural habitat - to each pixel (90 m^2 unit). The choices between each land use were determined by its relative effects on our three objectives (i.e., AP, BD, and WQ), and the weights assigned to each service for the given run. We defined our objective function as $F_{\boldsymbol{w}}(\boldsymbol{k}) = \sum_r w_r S_r(\boldsymbol{k})$, the sum of the value of each service r given a landscape $\boldsymbol{k}$, with weights w assigned to each service. Depending on the model, we used either exact (AP and WQ) or approximate (BD) functions, M_r, to calculate the change in the landscape service score given a change in a single pixel's land use, ($\boldsymbol{k}'$), and, thus, the marginal change in the total objective function: $\Delta F_{\boldsymbol{w}} =$

$\sum_r w_r M_r(\boldsymbol{k}, \boldsymbol{k}')$. In a given run, we chose an initial landscape, fixed the weight vector w, and then iteratively made a series of objective-improving alterations to the landscape by changing the land use assigned to particular pixels. In each iteration, we evaluated $\Delta F_{\boldsymbol{w}}$ for each potential transition, selected a given number of pixels, N, with the greatest positive marginal values, and changed the landscape correspondingly (N varies through the optimization, getting smaller as fewer positive changes remain). We used the landscape fully-restored to natural vegetation as the initial condition for the unconstrained optimization except for the Only BD frontier, where we used the current landscape as the starting condition. In this latter case, this resulted in more realistic landscapes given that the optimization's greedy heuristic tends to add or subtract from existing habitat patches rather than create new patches.

To find solutions that spanned the range of potential biophysical values for the modeled services, we varied the weight vectors and repeated the optimization for each combination of weights. We generated frontiers optimized for and with positive weights on two services (AP and only BD, or AP and only WQ), as well as with positive weights on all three services under low, medium and high weight for BD relative to WQ (see Table 1). Each frontier contains possible Pareto-efficient combinations of AP and ES under different weights for each service. After normalizing to account for unit differences, the relative weights for BD to WQ, respectively, were 1:0.5 for High BD frontier, 1:1 for Medium BD frontier, and 1:5 for Low BD frontier. In combination with the 0:1 and 1:0 frontiers, these intermediate weight values illustrate the range of potential three-way tradeoffs. The particular weights were chosen from a larger set of runs to be roughly evenly-spaced (or intermediate) between the two single-service curves (i.e., Only BD and Only WQ) to capture the gradient of the relative preferences between BD and WQ changes. We generated frontiers that depict the full range of biophysical possibilities for BD and WQ vs AP. This approach allows for planners or stakeholders to visualize the potential range of landscape outcomes under varying service preferences; if known, weights can be tailored to specific social preferences for nature conservation or can be informed through participatory engagement or monetary valuation.

We used slightly different procedures to generate the policy-constrained frontiers that had fixed targets for total natural cover (at property-or landscape-scales). While the unconstrained optimizations followed the above procedure exactly, when we imposed the 25% natural habitat rule at the PL or LL, we used a two-stage algorithm. We used the unconstrained solution for the current weight vector as the initial condition. Then the first step successively added or removed habitat based on $\Delta F_{\boldsymbol{w}}$ scores until exactly 25% was assigned at each scale. Second, we used a local-search improvement phase where a fraction of each property's habitat was cleared and reallocated to increase F_w. As with the unconstrained optimizations, we ran the optimization multiple times for LL and PL scenarios, varying the relative weights between the AP and ES objectives. See SI S§1.5–1.6 for details on the optimization procedure.

3. Results

3.1. Improvements to the current landscape

We find significant opportunities to improve both AP and ES relative to the current land use in the region. For the same level of profit as in the current landscape (~23 million USD), waterway nitrogen (N), phosphorus (P), and sediment (S) loads can be reduced by over 50%, 30%, and 7%, respectively, through the strategic placement of natural vegetation (Fig. 1, points A–E, see Table S6 for both tons and % changes).[2] Moreover, up to106 additional species could be supported, of which 95% are forest specialists and 80% are dietary specialists (Table S9A–C). Further,

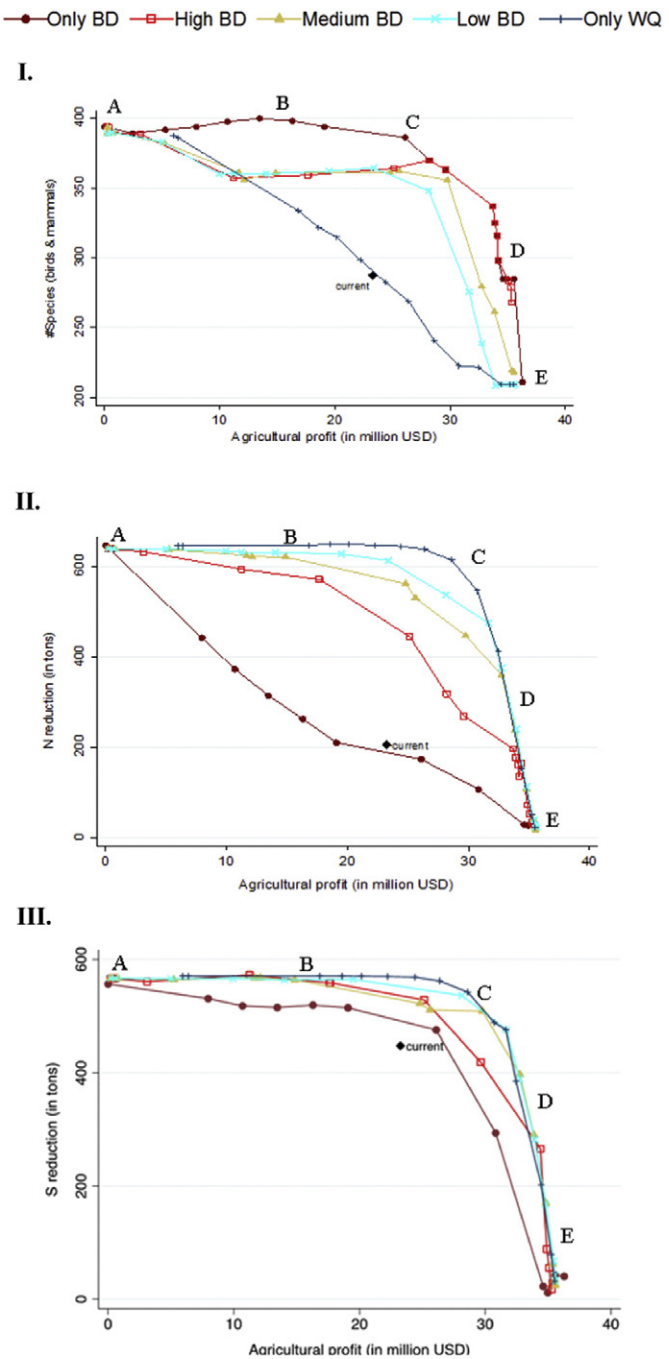


Fig. 1. Outcomes from the unconstrained optimizations between agricultural profit for sugarcane and cattle ranching and I) biodiversity, II) surface water nitrogen (N) loads, and III) surface water sediment (S) loads for the Ribeirão São Jerônimo watershed in Brazil. These efficiency frontiers depict the trade-offs between annual agricultural profit (AP) and an ecosystem service objective (calculated as a weighted sum of biodiversity (BD) and water quality (WQ)). Optimizations differed in whether all weight was on either BD or WQ (Only BD, Only WQ) or were jointly optimized with different weightings (Low, Medium, and High BD).[†] The reference for the reductions of N and S loads is a landscape under full agricultural production. The "current" point denotes the current land use. Points A–E illustrate the optimized landscape outcomes along main frontier segments (see Fig. 2 for the resulting land-use patterns).

[2] Points A–E refer to the different landscape optimizations along main segments of the efficiency frontiers (see Fig. 1).

[†] For the joint service optimizations, the depicted curves are not frontiers in the technical sense, but show the values of the component services. Frontiers slope upward in the Only BD frontier (point A to B) because there is an addition of agriculturally-adapted species (see SI S§2.1c); and we chose to leave these points in to have similar ranges for all curves although they are not actually Pareto efficient. The non-convexities occur in the joint-service frontiers (Low, Medium, and High BD) because the two-axis figure represents only part of the optimized objective function.

80–100% of all endemic species and 57–100% of those of conservation concern can be supported while maintaining current profit levels (Table S9C, S§2.1c).

Our analysis indicates that, by preserving only 20–24% of natural habitat, the region could support up to 97% of all bird and mammal species (point C, Only BD) or retain up to 91–95% of N, P and S loads (point C, Only WQ) relative to the fully restored (natural) landscape under single-service optimizations, while still increasing AP from current levels and without necessitating much more natural habitat (Fig. 1, Tables S6–7). Thus, strategic land-use planning can achieve improved outcomes for each service objective relative to the current baseline.

3.2. Agricultural profit and ecosystem services trade-offs

Along each frontier, agricultural expansion leads to higher AP with concomitant decreases in both BD and WQ (Fig. 1). In agricultural landscapes (point E), N, P, and S loadings to waterways are predicted to increase by 475–644, 43–56, 300–539 tons, respectively, relative to a natural landscape (point A) (Table S6); higher loads are predicted when less weight is placed on WQ. In addition, 140–191 bird and mammal species are predicted to be lost, with greater declines in larger-bodied species, habitat specialists, endemic species, species of conservation concern, and non-migratory birds (Table S9, Fig. S7). Only 19% of wetland specialists, 25% of forest specialists, and 27% of Cerrado specialists are predicted to be retained in a landscape fully converted to agriculture (Table S9A). In contrast, smaller-bodied species, species with greater habitat breadths, generalist species, species that prefer human-dominated land cover, nectivores, and migrants fare better under agricultural expansion (S§2.1c).

3.3. Biodiversity & water quality trade-offs

Less BD is retained in the region when planning prioritizes WQ, and vice versa. For example, when maintaining 20–25% natural habitat and optimizing for WQ, 107–145 (51–69%) fewer species are supported relative to the analogous scenario optimizing for BD (point C, Fig. 1, Table S6, S§2.1c). Under the same percent natural habitat, an additional 177–346 N tons, 15–29 P tons, and 90–123 S tons are predicted to end up in waterways, thereby reducing average WQ by 15–30%, when land use is optimized predominately for BD (Only BD and High BD frontiers) rather than for WQ (Medium BD, Low BD, and Only WQ frontiers) (point C, Fig. 1 and Table S6).

Overall, fewer trade-offs are detected between BD and S retention (Table S6), where all frontiers exhibit a concave shape even when no weight is attributed to WQ (Fig. 1 Panel III). In contrast, when land use targets only BD, the loss in N retention benefits is approximately linear with increasing AP (Fig. 1 Panel II), and vice versa (Fig. 1 Panel I). However, these relationships become concave when land allocation targets both BD and N retention (S§2.1b–c).

3.4. Multi-service planning

A large percentage of environmental quality improvement is possible by placing a non-zero weight on both BD and WQ (Table S6). At least 94% of species, 93% of S and 73% of N and P retention can be attained under joint optimization relative to when only one ES is maximized (points A–E, Fig. 1, Fig. S6).

Because the important natural habitat areas for these two objectives do not coincide, joint service planning is needed to reduce BD and WQ trade-offs (Fig. 2, S§2.1a). To maximize BD, natural remnants are largely comprised of Cerradão, followed by semi-deciduous forest (Fig. S5), because these habitat types have the highest habitat suitability for species (Table S3). Natural habitat is also concentrated in large and less fragmented patches (Fig. 2). For example, the Only BD landscape has 2.8× more total core area, 3.7× less edge area, and core patches that are 31× larger relative to the Only WQ landscape (point C, Table S12). This habitat pattern arises because species are predicted to have higher persistence when habitat is less fragmented, more connected, and comprises larger suitable habitat patches (Polasky et al., 2008).

In contrast, the areas important for WQ provision are concentrated along water bodies and on steep slopes because these areas have the greatest filtering potential and/or protect critical pollutant loading sites (Fig. 2). Wetlands and riparian forests, which are found in these locations (Fig. S3), and have higher pollutant retention capabilities relative to other land cover types (S§1.3), are preferentially preserved when WQ is targeted. For example, at points B–C, an average of 72–73% of all possible wetlands and forests are retained relative to only 9% and 29% of all possible cerradão and cerrado, respectively (Table S7, Only WQ frontier).

3.5. Service thresholds

The slope of the efficiency frontiers, which indicates the opportunity cost of providing an additional unit of ES, is not constant. When ≥50% of the watershed is set aside for conservation (point B), a further addition of natural vegetation to maximize either BD or WQ (to reach point A, Fig. 1) results in small gains in species and in N, P, and S retention, but significant loss of AP: 62–100% and 43–83% loss in profit in the Only BD and Only WQ frontiers, respectively (Table S6). Conversely, when the watershed is allocated to agriculture (point E), strategically conserving only 10% of habitat (to reach point D) can support up to 75% of all possible species (adding 87 species) and can retain ~64%, 52%, and 67% of N, P, and S loads at the expense of <8% foregone AP (Table S6).

All frontiers exhibit a threshold at 20–25% natural vegetation that marks the point where the marginal costs change drastically in magnitude for all services. When agriculture spans >75% of the watershed, gains in AP can be obtained at only a high cost to BD and WQ. Conversely, <75% habitat clearance, the ES cost of agricultural production is relatively low (point C, Fig. 1). The detected 25% critical habitat threshold for both BD and ES is consistent with the FC requirements in the region (Fig. 3).

3.6. Forest Code compliance efficiencies

With the same amount of natural habitat as the current landscape, FC compliance optimized at PL and LL scales can generate additional ~5 million/year USD in AP and improve aggregate WQ by 18–22% when planning for this service (Fig. 3 Panel VI, Table S10). At both planning scales, placing higher weights on WQ generates higher pollutant retention rates and results in landscapes where habitats are concentrated along riparian areas (Fig. 4, S§2.2b). Alternatively, when targeting BD, FC compliance can support an additional 2 to 88 species (Table S10, S§2.2c), with the larger gains under LL planning (Fig. 3 Panel I). The greatest ES improvements occur when FC compliance places equal weights on both BD and WQ.

Our models predict that LL compliance can lead to outcomes that approximate the unconstrained frontiers and are, therefore, the best possible for the region under the 25% habitat requirement. Smaller reductions in N, P, and S rates are found under PL relative to LL planning regardless of the service weight (Fig. 3). These gains are even more pronounced for BD: with LL planning boosting species richness by 9.1–34.4% versus only 4.3–9.6% for average WQ (Table S10). Relative to PL, LL planning can support up to an additional 72 species and comprise at least 97% of species expected under unconstrained planning with similar trait composition (S§2.2c). Fewer and different species are supported under PL planning because habitat is more fragmented, with less habitat core and smaller patches with more edge (Fig. 4, S§2.2a).

4. Discussion

Our results underscore that strategic multi-objective land use planning at larger spatial scales provides clear opportunities to improve

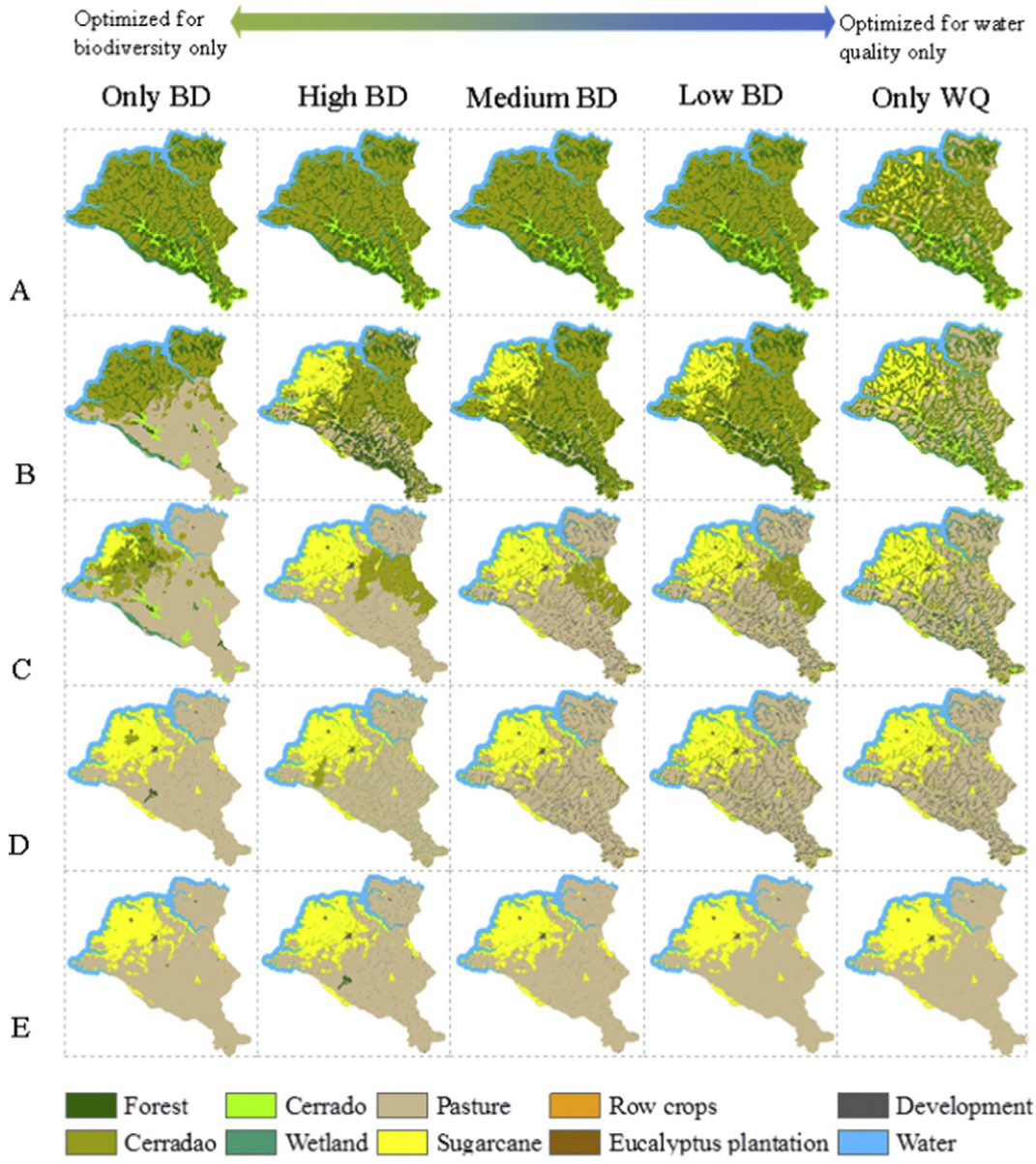


Fig. 2. Land-use patterns corresponding to the coordinate points along each unconstrained efficiency frontier (points A–E, Fig.1) based on different preferences (or weightings) for biodiversity and water quality. We optimized land based on the dominant agricultural land uses (cattle ranching and sugarcane production) and natural habitat types (wetlands, forest, cerradão, or cerrado) in the region. Although other agricultural land uses exist (row crops and plantations) they were not modeled given they make of <1% of land area and not forecasted to expand in the region. We assumed that all areas in the study watershed, with the exception of water bodies and infrastructure development, can be converted to cattle ranching, sugarcane production, or natural habitat (see Methods and SI for further details).

both economic and environmental outcomes. This finding is particularly important to areas of high biodiversity and high potential for agricultural expansion, like the Brazilian Cerrado (Klink and Machado, 2005). We find that our study region can generate higher agricultural profit (AP) while also supporting substantial improvements in both biodiversity (BD) and water quality (WQ) compared to the current land use. Given that inefficient land use allocations have been found in other systems (e.g., Polasky et al., 2008), we propose that many landscapes, similar to our region, have opportunities to increase both agricultural development and ecosystem services (ES) despite their trade-offs (Power, 2010). By examining potential benefits of land-use changes under a full range of preferences and at different planning scales, our framework identifies both "win-win" and "small loss-big gain" opportunities, both of which are essential to better balance economic development with long-term ecosystem function (DeFries et al., 2004).

Our findings have important implications for land use planning and sustainability policy in Brazil and globally. First, identifying win-win and small loss-big gain outcomes requires an improved understanding of non-linear ecosystem changes and thresholds in landscapes, which are expected based on theory, but our understanding of them is limited for real-world systems (Scheffer et al., 2012). The shape of the responses of BD and ES to agricultural expansion and where tipping points lie will inform effective land use strategies to help reconcile agriculture with conservation (Chaplin-Kramer et al., 2015; Fischer et al., 2014). Concave relationships, as predominately predicted by our models, suggest that agricultural expansion can occur at little cost to both BD and WQ under strategic habitat conservation until ~20–25% natural vegetation remains in the watershed. This finding is consistent with the minimum habitat thresholds detected for species in the Brazilian Atlantic Forest (Banks-Leite et al., 2014) and elsewhere (Huggett, 2005), and is in line with development impacts on stream conditions (Brabec, 2009).

On the other hand, when agriculture expands without spatially targeting environmental benefits, our models predict a linear loss in both BD and N retention. Linear (and convex) relationships were also

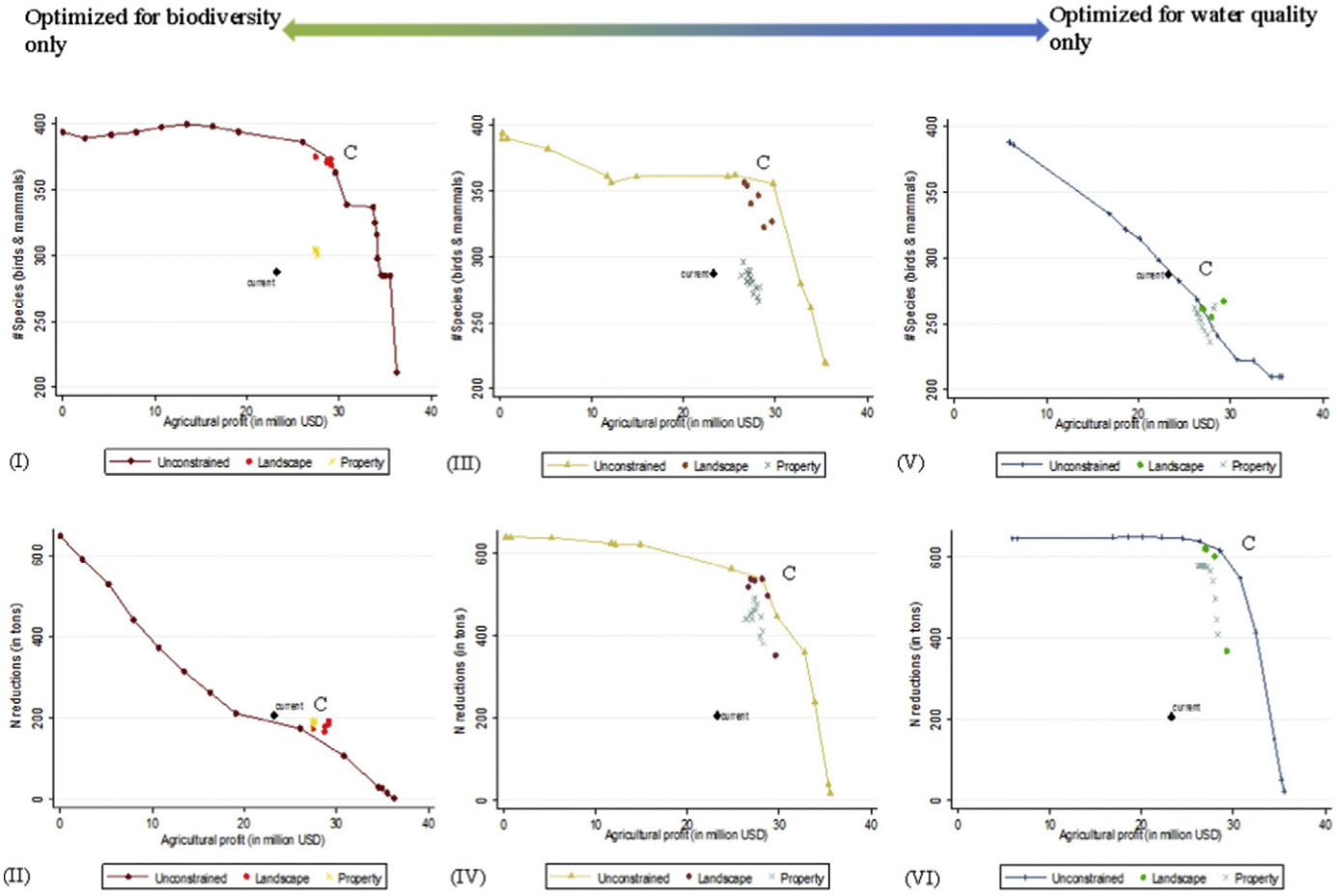


Fig. 3. Forest Code (FC) compliance at the property-level (PL) and landscape-level (LL) in relation to analogous unconstrained optimizations. Panels I–II refer to the single-service optimization for biodiversity (Only BD frontier); III–IV to the joint-service optimization (Medium BD frontier), and V–VI to the single-service optimization for water quality (Only WQ frontier). Point "C" on the unconstrained frontier corresponds to the 25% habitat requirement of the FC at the two scales. The"current" point denotes the current land use. The "property" and "landscape" and points approximate the FC compliance frontiers for PL and LL, respectively, under optimizations with different relative weights on AP, BD, and WQ.

detected by Chaplin-Kramer et al. (2015) that simulated habitat conversion patterns of agricultural expansion on BD and carbon storage in Mato Grosso, Brazil. Our results further indicate that the FC habitat requirements fall very close to a pivotal threshold in our region, which suggest that small reductions in natural vegetation can result in precipitous ES declines. The presence of pronounced thresholds and the potential for steep declines when ES are not targeted raise questions about FC performance without full and optimal compliance: which is the norm in many regions in Brazil and may be exacerbated by the 2012 FC revisions that allow additional deforestation in the Cerrado (Soares-Filho et al., 2014). A cautionary response by policy-makers could be to minimize the potential of reaching undesirable thresholds and ES losses by requiring and/or incentivizing the protection and restoration of higher percentages of natural vegetation in sensitive landscapes. For example, the State of Piauí increased the required percentage of LRs in rural properties from the traditional 20% to 30% for Cerrado vegetation (Law 5699/2007).[3]

Second, our case study underscores the ability to mitigate not only the trade-offs between AP and BD conservation, but also other ES. Research on the effects of agricultural expansion has focused on minimizing impacts on BD and has relied on trade-off analyses between commodity production and BD metrics to determine preferable land use strategies (e.g., Phalan et al., 2011). This emphasis has been criticized as limited in utility and impractical (Fischer et al., 2014; Kremen, 2015; Tscharntke et al., 2012). As we attempt here, Fischer et al. (2014) argues that more than two environmental goods, and varying preferences, should be accounted for to provide a fuller assessment of the trade-offs between alternative land uses.

We focus on BD and WQ given the legal precedent in Brazil (Soares-Filho et al., 2014) and detect substantial trade-offs between these two objectives because the geographic distributions of important land areas do not coincide, as found by other studies (e.g., Naidoo et al., 2008; Qiu and Turner, 2013). But we expand upon previous work and demonstrate that joint optimization for multiple ES objectives can attain on average > 80% of both BD and WQ objectives and improve overall environmental quality. Admittedly, BD and WQ are only two of a multitude of benefits and trade-offs that should be considered when evaluating the impacts of agricultural expansion. In addition, the trade-offs between BD and other ES depend on their degree of spatial concordance, and may exhibit greater synergies than we detected for ES that are tightly associated with natural vegetation communities and whose provisioning depends on high levels of species (Cardinale et al., 2012). Our optimization framework can be extended to include other ES, such as natural pest control, pollination, timber production, and carbon storage, where locally relevant and when data exist, and to account for known social preferences, to more fully design multi-functional landscapes.

Third, we find that landscape-scale planning can benefit both BD and WQ, without imposing additional costs to agriculture, relative to farm-by-farm planning that is the norm in agricultural landscapes (Swift et al., 2004). That LL planning can generate benefits to agricultural

[3] http://legislacao.pi.gov.br/legislacao/default/ato/13386.

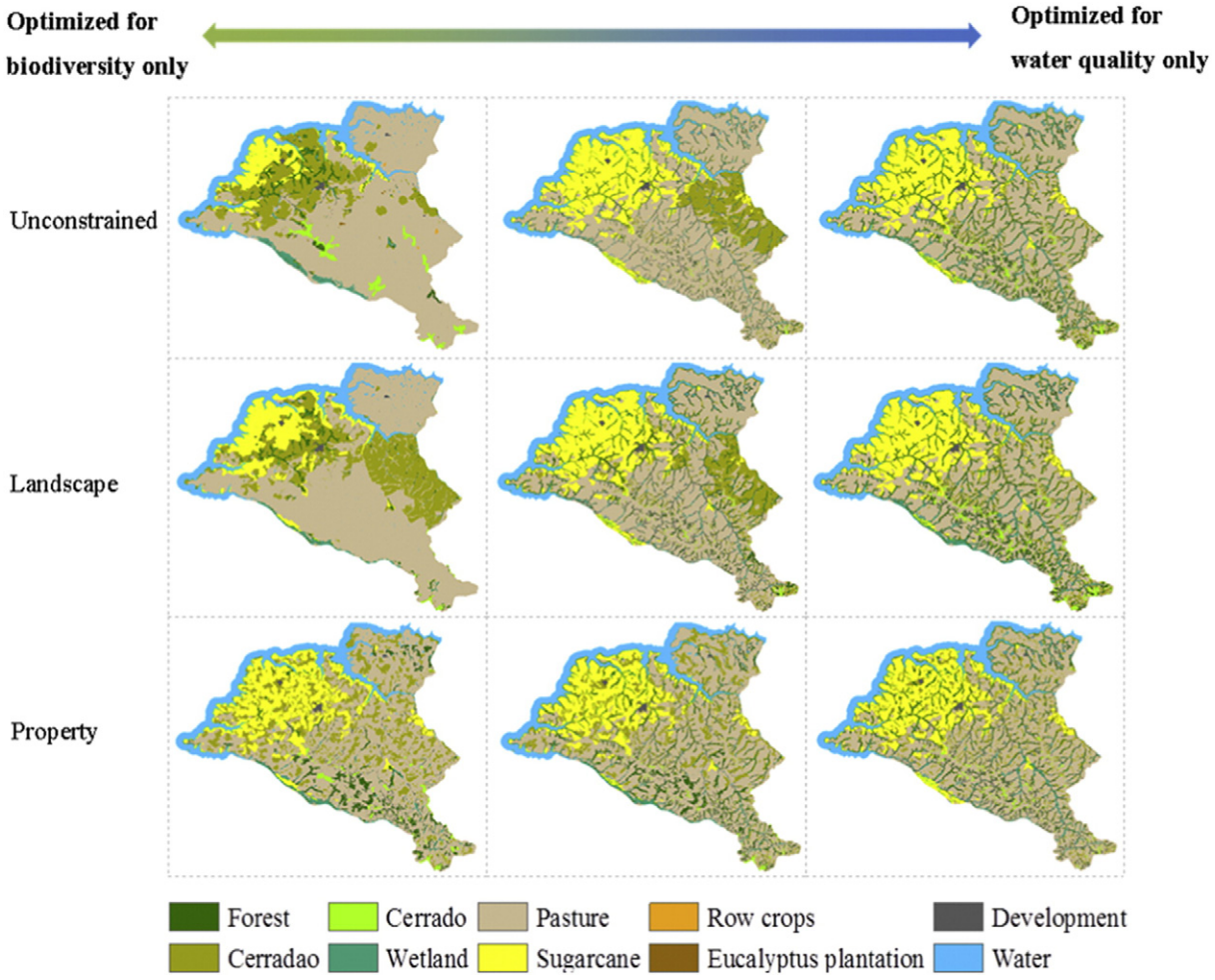


Fig. 4. Land use patterns resulting from the property-, landscape- and unconstrained optimizations for biodiversity only, joint biodiversity and water quality, and water quality only. All depicted landscapes mimic the Forest Code requirements of 25% of the watershed area being under natural vegetation and correspond to point C in Fig. 3.

producers is consistent with previous studies. In the case of pollination, an ES that can benefit crop yields, Cong et al. (2014) demonstrates that landscape-scale management boosts farm profits relative to farm-level practices. In the same watershed as this study, Kennedy et al. (2016) reveals that landscape-level FC compliance can reduce costs to sugarcane producers and provide ecosystem services, even when land use decisions are based on maximizing sugarcane production profits (without targeting ES benefits). Large-scale compliance can be achieved under FC provisions that allow land owners to compensate (offset) their legal requirements within the same biome by protecting habitats (established or regenerating natural vegetation) on other properties through land acquisition or leasing; donating lands within protected areas to the government; or purchasing an Environmental Reserve Quota (CRA) (tradable legal title to surplus native vegetation) (Silva and Ranieri, 2014; Soares-Filho et al., 2014). Although there is ongoing debate about the appropriate scale for mitigation in Brazil and in other countries, a more restricted geographic scale than the biome, such as a hydrographic basin (as done in our modeling), is recommended to better ensure ecological equivalency and social equality in the compensation of biodiversity and ecosystem services (Silva et al., 2012; Silva and Ranieri, 2014; Sparovek et al., 2012b; Tallis et al., 2015).

Our case study highlights that the planning scale greatly impacts the outcomes of land use design, but the magnitude depends on the characteristics of each ES. For BD, landscape planning is predicted to benefit bird and mammal groups that are threatened globally by habitat conversion: larger-bodied species, habitat and dietary specialists, endemic species, and species of conservation concern (Davidson et al., 2009; Sekercioğlu, 2012). The reason is that optimized landscapes are comprised of larger, more intact and connected patches that are farther from human disturbance, which have been empirically shown to improve species diversity and communities at regional (or gamma) scales (e.g., Haddad et al., 2015). To maximize WQ, natural habitat is consistently concentrated along riparian areas at both property and landscape scales, which suggests that farm-level decision-making, as regulated by the FC, has the potential to better meet WQ than BD objectives. Yet, WQ improvements are still possible at larger spatial scales because of the greater flexibility to place habitats in the best spatial configuration that spans more than single farm. Thus, ES benefits are likely from LL planning when their biophysical requirements operate at geographic extents larger than a single farm and are unevenly distributed across a region (Stallman, 2011; Swift et al., 2004). Although the benefits of a landscape design for ES has been less studied than for BD (Mitchell et al., 2015), services like pollination, pest control, flood control, and nature recreation, among others, are expected to improve when land use is coordinated across multiple properties in agricultural settings (Stallman, 2011).

Our results hinge on the assumption that private lands can be converted to the most profitable use and/or the most ES-delivering habitat types. This assumption may be more tenable under conditions similar to those in our region where landscapes dominated by cattle farms are being converted to commercial crop production where profitable while habitats are being protected and restored as required by law (S§1.1). In addition, our modeling focused on the spatial arrangement of natural habitats within a human-modified landscape to optimize

both agriculture and conservation under existing farming practices. Future extensions of this work could examine the additional benefits of increasing agricultural efficiency and adopting agro-ecological farming techniques, such as conservation agriculture, crop rotation, natural pest management, organic fertilization, improved fodder grass selection, rotational grazing, and integrated crop-livestock systems, which may further mitigate negative impacts and prevent displacement of agricultural activities elsewhere (Kremen, 2015; Sparovek et al., 2007; Strassburg et al., 2014).

In order to identify win-win and small loss-big gain outcomes in real-world systems (DeFries et al., 2004), it is imperative to increase the awareness and understanding about the trade-offs and thresholds in the provision of ES and economic profit with case studies (Groffman et al., 2006). Modeling approaches, like our optimization framework, that assess multiple economic activities along with multiple ecosystem benefits, and account for different preferences, can help evaluate the potential performance of land use policies like the FC in Brazil and others elsewhere (O'Farrell and Anderson, 2010). However, mechanisms, like payment for ecosystem services, tradeable environmental reserve quotas, and market incentives, need to be in place to foster land-use planning across properties to implement optimal landscapes that balance both private economic and public environmental benefits (Bateman et al., 2015; Cong et al., 2014; Polasky et al., 2014). To inform the optimal design of land use policy or incentive mechanisms in practice, future modeling work should also seek to incorporate influential spatial interactions and potential dynamic feedbacks between conservation and development (Armsworth et al., 2006), and to consider land use transition constraints, the distributions of costs and benefits, and the role of uncertainty (see S§3 for details) (Fischer et al., 2009).

Author contributions

C.M.K., P.L.H., L.B., J.K. conceived and designed the study; L.B., D.A.M., C.M.K, K.S., M.M., collected the data; P.L.H., L.B., C.M.K., D.A.M., K.S., J.S.E., M.M. conducted the modeling and analysis; C.M.K, D.A.M., P.L.H., K.S. produced the figures and tables; S.P. provided guidance on optimization procedures; P.H. provided data and input on the hydrologic modeling; C.M.K., K.S., E.M.V., P.F.D., A.D.D., C.H.S. provided data and guidance on the biodiversity modeling; E.M.U. informed the business context; C.M.K., D.A.M., P.L.H., J.K., designed and wrote the paper; C.M.K., P.L.H., J.K., D.A.M., E.M.V., E.M.U., S.P., L.B., K.S., P.H. revised the paper.

Acknowledgements

We are grateful to E. Okumura, E. Garcia, C. Pereira, and J. Pereira for input on the sugarcane modeling. L. Azevedo, J. Guimarães, K. Voss, I. Alameddine, S. Thompson, and B. Keeler for input on the hydrologic modeling; E. Lonsdorf and E. Nelson for input on the biodiversity and optimization modeling. Funding was provided by The Dow Chemical Company Foundation, The Dow Chemical Company, The Nature Conservancy, Anne Ray Charitable Trust and The 3M Foundation.

References

Armsworth, P.R., Daily, G.C., Kareiva, P., Sanchirico, J.N., 2006. Land market feedbacks can undermine biodiversity conservation. Proc. Natl. Acad. Sci. U.S.A. 103, 5403–5408.

Baccini, A., Goetz, S., Walker, W., Laporte, N., Sun, M., Sulla-Menashe, D., Hackler, J., Beck, P., Dubayah, R., Friedl, M., 2012. Estimated carbon dioxide emissions from tropical deforestation improved by carbon-density maps. Nat. Clim. Chang. 2, 182–185.

Banks-Leite, C., Pardini, R., Tambosi, L.R., Pearse, W.D., Bueno, A.A., Bruscagin, R.T., Condez, T.H., Dixo, M., Igari, A.T., Martensen, A.C., 2014. Using ecological thresholds to evaluate the costs and benefits of set-asides in a biodiversity hotspot. Science 345, 1041–1045.

Bateman, I.J., Coombes, E., Fitzherbert, E., Binner, A., Bad'ura, T., Carbone, C., Fisher, B., Naidoo, R., Watkinson, A.R., 2015. Conserving tropical biodiversity via market forces and spatial targeting. Proc. Natl. Acad. Sci. U.S.A. 112, 7408–7413.

Bateman, I.J., Harwood, A.R., Mace, G.M., Watson, R.T., Abson, D.J., Andrews, B., Binner, A., Crowe, A., Day, B.H., Dugdale, S., 2013. Bringing ecosystem services into economic decision-making: land use in the United Kingdom. Science 341, 45–50.

Brabec, E.A., 2009. Imperviousness and land-use policy: toward an effective approach to watershed planning. J. Hydrol. Eng. 14, 425–433.

Brosi, B.J., Armsworth, P.R., Daily, G.C., 2008. Optimal design of agricultural landscapes for pollination services. Conserv. Lett. 1, 27–36.

Cardinale, B.J., Duffy, J.E., Gonzalez, A., Hooper, D.U., Perrings, C., Venail, P., Narwani, A., Mace, G.M., Tilman, D., Wardle, D.A., 2012. Biodiversity loss and its impact on humanity. Nature 486, 59–67.

Carpenter, S.R., Mooney, H.A., Agard, J., Capistrano, D., DeFries, R.S., Díaz, S., Dietz, T., Duraiappah, A.K., Oteng-Yeboah, A., Pereira, H.M., Perrings, C., Reid, W.V., Sarukhan, J., Scholes, R.J., Whyte, A., 2009. Science for managing ecosystem services: beyond the millennium ecosystem assessment. Proc. Natl. Acad. Sci. U. S. A. 106, 1305–1312.

Chaplin-Kramer, R., Sharp, R.P., Mandle, L., Sim, S., Johnson, J., Butnar, I., Canals, L.M.I., Eichelberger, B.A., Ramler, I., Mueller, C., 2015. Spatial patterns of agricultural expansion determine impacts on biodiversity and carbon storage. Proc. Natl. Acad. Sci. U.S.A. 112, 7402–7407.

Cong, R.-G., Ekroos, J., Smith, H.G., Brady, M.V., 2016. Optimizing intermediate ecosystem services in agriculture using rules based on landscape composition and configuration indices. Ecol. Econ. 128, 214–223.

Cong, R.-G., Smith, H.G., Olsson, O., Brady, M., 2014. Managing ecosystem services for agriculture: will landscape-scale management pay? Ecol. Econ. 99, 53–62.

Davidson, A.D., Hamilton, M.J., Boyer, A.G., Brown, J.H., Ceballos, G., 2009. Multiple ecological pathways to extinction in mammals. Proc. Natl. Acad. Sci. U. S. A. 106, 10702–10705.

DeFries, R.S., Foley, J.A., Asner, G.P., 2004. Land-use choices: balancing human needs and ecosystem function. Front. Ecol. Environ. 2, 249–257.

Dow Chemical, 2008. EIA-RIMA Usina Santa Vitória (Referencia: 0078457). Dow Chemical.

Fischer, J., Abson, D.J., Butsic, V., Chappell, M.J., Ekroos, J., Hanspach, J., Kuemmerle, T., Smith, H.G., Wehrden, H., 2014. Land sparing versus land sharing: moving forward. Conserv. Lett. 7, 149–157.

Fischer, J., Peterson, G.D., Gardner, T.A., Gordon, L.J., Fazey, I., Elmqvist, T., Felton, A., Folke, C., Dovers, S., 2009. Integrating resilience thinking and optimisation for conservation. Trends Ecol. Evol. 24, 549–554.

Gibbs, H., Ruesch, A., Achard, F., Clayton, M., Holmgren, P., Ramankutty, N., Foley, J., 2010. Tropical forests were the primary sources of new agricultural land in the 1980s and 1990s. Proc. Natl. Acad. Sci. U.S.A. 107, 16732–16737.

Groffman, P.M., Baron, J.S., Blett, T., Gold, A.J., Goodman, I., Gunderson, L.H., Levinson, B.M., Palmer, M.A., Paerl, H.W., Peterson, G.D., 2006. Ecological thresholds: the key to successful environmental management or an important concept with no practical application? Ecosystems 9, 1–13.

Groot, J.C., Rossing, W.A., Jellema, A., Stobbelaar, D.J., Renting, H., Van Ittersum, M.K., 2007. Exploring multi-scale trade-offs between nature conservation, agricultural profits and landscape quality—a methodology to support discussions on land-use perspectives. Agric. Ecosyst. Environ. 120, 58–69.

Haddad, N.M., Brudvig, L.A., Clobert, J., Davies, K.F., Gonzalez, A., Holt, R.D., Lovejoy, T.E., Sexton, J.O., Austin, M.P., Collins, C.D., 2015. Habitat fragmentation and its lasting impact on Earth's ecosystems. Sci. Adv. 1, e1500052.

Hansen, M.C., Potapov, P.V., Moore, R., Hancher, M., Turubanova, S., Tyukavina, A., Thau, D., Stehman, S., Goetz, S., Loveland, T., 2013. High-resolution global maps of 21st-century forest cover change. Science 342, 850–853.

Huggett, A.J., 2005. The concept and utility of 'ecological thresholds' in biodiversity conservation. Biol. Conserv. 124, 301–310.

Jenkins, C.N., Pimm, S.L., Joppa, L.N., 2013. Global patterns of terrestrial vertebrate diversity and conservation. Proc. Natl. Acad. Sci. U.S.A. 110, E2602–E2610.

Kennedy, C.M., Baumgarten, L., Matsumoto, M., Evans, J.S., Miteva, D.A., 2014. Geospatial Data Applied to the Brazilian Cerrado. The Nature Conservancy:p. 28. http://nature.org/TNC-Dow-Brazil-Geospatial-Data-Description.

Kennedy, C.M., Miteva, D.A., Baumgarten, L., Hawthorne, P.L., Sochi, K., Polasky, S., Oakleaf, J.R., Uhlhorn, E.M., Kiesecker, J., 2016. Bigger is better: improved nature conservation and economic returns from landscape-level mitigation. Sci. Adv. 2. http://advances.sciencemag.org/content/advances/2/7/e1501021.full.pdf.

Klink, C.A., Machado, R.B., 2005. Conservation of the Brazilian cerrado. Conserv. Biol. 19, 707–713.

Koh, L.P., Ghazoul, J., 2010. Spatially explicit scenario analysis for reconciling agricultural expansion, forest protection, and carbon conservation in Indonesia. Proc. Natl. Acad. Sci. U.S.A. 107, 11140–11144.

Kremen, C., 2015. Reframing the land-sparing/land-sharing debate for biodiversity conservation. Ann. N. Y. Acad. Sci. 1355, 52–76.

Lapola, D.M., Schaldach, R., Alcamo, J., Bondeau, A., Koch, J., Koelking, C., Priess, J.A., 2010. Indirect land-use changes can overcome carbon savings from biofuels in Brazil. Proc. Natl. Acad. Sci. U. S. A. 107, 3388–3393.

Law, E.A., Meijaard, E., Bryan, B.A., Mallawaarachchi, T., Koh, L.P., Wilson, K.A., 2015. Better land-use allocation outperforms land sparing and land sharing approaches to conservation in Central Kalimantan, Indonesia. Biol. Conserv. 186, 276–286.

Lichtenstein, M.E., Montgomery, C.A., 2003. Biodiversity and timber in the Coast Range of Oregon: inside the production possibility frontier. Land Econ. 79, 56–73.

Mitchell, M.G., Suarez-Castro, A.F., Martinez-Harms, M., Maron, M., McAlpine, C., Gaston, K.J., Johansen, K., Rhodes, J.R., 2015. Reframing landscape fragmentation's effects on ecosystem services. Trends Ecol. Evol. 30, 190–198.

Naidoo, R., Balmford, A., Costanza, R., Fisher, B., Green, R.E., Lehner, B., Malcolm, T.R., Ricketts, T.H., 2008. Global mapping of ecosystem services and conservation priorities. Proc. Natl. Acad. Sci. U. S. A. 105, 9495–9500.

Nelson, E., Mendoza, G., Regetz, J., Polasky, S., Tallis, H., Cameron, D., Chan, K.M., Daily, G.C., Goldstein, J., Kareiva, P.M., 2009. Modeling multiple ecosystem services, biodiversity conservation, commodity production, and tradeoffs at landscape scales. Front. Ecol. Environ. 7, 4–11.

O'Farrell, P.J., Anderson, P.M.L., 2010. Sustainable multifunctional landscapes: a review to implementation. Curr. Opin. Environ. Sustain. 2, 59–65.
Phalan, B., Onial, M., Balmford, A., Green, R.E., 2011. Reconciling food production and biodiversity conservation: land sharing and land sparing compared. Science 333, 1289–1291.
Polasky, S., Lewis, D.J., Plantinga, A.J., Nelson, E., 2014. Implementing the optimal provision of ecosystem services. Proc. Natl. Acad. Sci. U.S.A. 111, 6248–6253.
Polasky, S., Nelson, E., Camm, J., Csuti, B., Fackler, P., Lonsdorf, E., Montgomery, C., White, D., Arthur, J., Garber-Yonts, B., Haight, R., Kagan, J., Starfield, A., Tobalske, C., 2008. Where to put things? Spatial land management to sustain biodiversity and economic returns. Biol. Conserv. 141, 1505–1524.
Power, A.G., 2010. Ecosystem services and agriculture: tradeoffs and synergies. Philos. Trans. R. Soc., B 365, 2959–2971.
Qiu, J., Turner, M.G., 2013. Spatial interactions among ecosystem services in an urbanizing agricultural watershed. Proc. Natl. Acad. Sci. U.S.A. 110, 12149–12154.
Ramankutty, N., Evan, A.T., Monfreda, C., Foley, J.A., 2008. Farming the planet: 1. Geographic distribution of global agricultural lands in the year 2000. Glob. Biogeochem. Cycles 22, GB1003.
Scheffer, M., Carpenter, S.R., Lenton, T.M., Bascompte, J., Brock, W., Dakos, V., Van De Koppel, J., Van De Leemput, I.A., Levin, S.A., Van Nes, E.H., 2012. Anticipating critical transitions. Science 338, 344–348.
Sekercioğlu, C.H., 2012. Bird functional diversity and ecosystem services in tropical forests, agroforests and agricultural areas. J. Ornithol. 153, 153–161.
Silva, J.A.A.d., Nobre, A., Manzatto, C., Joly, C., Rodrigues, R., Skorupa, L., Nobre, C., Ahrens, S., May, P., Sá, T., 2012. O Código Florestal e a Ciência: Contribuições para o diálogo. Sociedade Brasileira para o Progresso da Ciência (SBPC) and Academia Brasileira de Ciências (ABC), São Paulo, p. 124.
Silva, J.S.d., Ranieri, V.E.L., 2014. O mecanismo de compensação de reserva legal e suas implicações econômicas e ambientais. Ambiente & Sociedade 17, 115–132.
Soares-Filho, B., Rajão, R., Macedo, M., Carneiro, A., Costa, W., Coe, M., Rodrigues, H., Alencar, A., 2014. Cracking Brazil's Forest Code. Science 344, 363–364.
Sparovek, G., Berndes, G., Barretto, A., Klug, I.L.F., 2012a. The revision of the Brazilian Forest Act: increased deforestation or a historic step towards balancing agricultural development and nature conservation? Environ. Sci. Pol. 16, 65–72.
Sparovek, G., Berndes, G., Egeskog, A., de Freitas, F.L.M., Gustafsson, S., Hansson, J., 2007. Sugarcane ethanol production in Brazil: an expansion model sensitive to socioeconomic and environmental concerns. Biofuels Bioprod. Biorefin. 1, 270–282.
Sparovek, G., Berndes, G., Giaroli de Oliveira Pereira Barretto, A., Fröhlich Klug, I.L.F., 2012b. The revision of the Brazilian Forest Act: increased deforestation or a historic step towards balancing agricultural development and nature conservation? Environ. Sci. Pol. 16, 65–72.
Stallman, H.R., 2011. Ecosystem services in agriculture: determining suitability for provision by collective management. Ecol. Econ. 71, 131–139.
Strassburg, B.B., Latawiec, A.E., Barioni, L.G., Nobre, C.A., da Silva, V.P., Valentim, J.F., Vianna, M., Assad, E.D., 2014. When enough should be enough: improving the use of current agricultural lands could meet production demands and spare natural habitats in Brazil. Glob. Environ. Chang. 28, 84–97.
Swift, M.J., Izac, A.-M.N., van Noordwijk, M., 2004. Biodiversity and ecosystem services in agricultural landscapes—are we asking the right questions? Agric. Ecosyst. Environ. 104, 113–134.
Tallis, H., Kennedy, C.M., Ruckelshaus, M., Goldstein, J., Kiesecker, J.M., 2015. Mitigation for one & all: an integrated framework for mitigation of development impacts on biodiversity and ecosystem services. Environ. Impact Assess. Rev. 55, 21–34.
Tallis, H.T., Ricketts, T., Guerry, A.D., Wood, S.A., Sharp, R., Nelson, E., Ennaanay, D., Wolny, S., Olwero, N., Vigerstol, K., Pennington, D., Mendoza, G., Aukema, J., Foster, J., Forrest, J., Cameron, D., Arkema, K., Lonsdorf, E., Kennedy, C., Verutes, G., Kim, C.K., Guannel, G., Papenfus, M., Toft, J., Marsik, M., Bernhardt, J., Griffin, R., Glowinski, K., Chaumont, N., Perelman, A., Lacayo, M., 2013. InVEST 2.5.6 User's Guide: Integrated Valuation of Ecosystem Services and Tradeoffs. Natural Capital Project Stanford, Palo Alto, CA, p. 155.
Tilman, D., Balzer, C., Hill, J., Befort, B.L., 2011. Global food demand and the sustainable intensification of agriculture. Proc. Natl. Acad. Sci. U.S.A. 108, 20260–20264.
Tscharntke, T., Clough, Y., Wanger, T.C., Jackson, L., Motzke, I., Perfecto, I., Vandermeer, J., Whitbread, A., 2012. Global food security, biodiversity conservation and the future of agricultural intensification. Biol. Conserv. 151, 53–59.