Using optimization methods to align food production and biodiversity conservation beyond land sharing and land sparing

VAN BHTSC1,4 AND TOBIAS KUEMBERLE2,3

1Department of Environmental Science, Policy, and Management, University of California, Berkeley, California 94720 USA
2Geography Department, Humboldt-University Berlin, Unter den Linden 6, 10099 Berlin, Germany
3Integrative Research Institute on Transformations in Human-Environment Systems (IRI THESys), Humboldt-University Berlin, Unter den Linden 6, 10099 Berlin, Germany

Abstract. Aligning food production with biodiversity conservation is one of the greatest challenges of our time. One framing of this challenge is the land-sharing vs. land-sparing debate. Much empirical research has focused on identifying the relationship between agricultural yields and species populations, and using the relative number of species with particular relationships to inform landscape-level management. We feel this is misguided, as such an approach does not guarantee the existence of every species of conservation concern. Here, we show that constrained optimization methods can be used to identify landscape-level solutions which maximize agricultural yields and populations for any number of species. Our results suggest that the relative number of species with particular yield–density curves is not a good indicator as to how landscapes should be managed. Likewise, choosing between blanket sharing or sparing strategies leads to suboptimal outcomes at the landscape scale in many cases. Our framework makes maximum use of the rich information contained in yield–density curves to move beyond black-and-white choices and toward more nuanced, context-specific solutions to aligning biodiversity conservation and agricultural production. Such optimal landscapes will likely have features of both sharing and sparing strategies.

Key words: agriculture; biodiversity; conservation; land sharing; land sparing; optimization.

INTRODUCTION

Global biodiversity is in peril and agricultural expansion and intensification are among the main drivers of this crisis (Millennium Ecosystem Assessment 2005, CBD 2010, Barnosky et al. 2011). The question of how to best conserve biodiversity while producing enough food, feed, and bioenergy for human use is therefore a leading question in sustainability and conservation science (West et al. 2010, Foley et al. 2011). Research about how to minimize trade-offs between these often contrasting goals has regularly been framed within the context of the land-sparing vs. land-sharing debate (Green et al. 2005, Laurance et al. 2012, Tscharntke et al. 2012, Phalan et al. 2014). Land sparing here refers to landscapes where agricultural production takes place in a yield-maximizing manner, using less land and thus ideally sparing land for nature. Land sharing, in contrast, refers to landscapes where lower-intensity agriculture and biodiversity largely co-occur, but that contain little untouched land. While this framework has been criticized for insufficiently addressing the many externalities of intensive agricultural production, and the complex linkages between agricultural production, food security, and food sovereignty (Chappell and LaValle 2009, Fischer et al. 2014), the general framework has remained a touchstone for research on trade-offs between agricultural production and biodiversity.

The key theoretical insight of the land-sharing vs. land-sparing debate is that for a given level of agricultural production, individual species’ populations can be maximized based upon their yield–density curves, i.e., curves which show the relationship between agricultural yield on one axis and the species’ population size on the other (Fig. 1; Green et al. 2005). Species with a convex (also referred to as concave down; Godfray 2011, Gabriel et al. 2013) yield–density curve experience drastic population declines as agricultural intensity increases, and thus have larger populations in land-
sparing landscapes (we refer to these as sparing species, others call them loser species or land-sparing species; Godfray 2011, Phalan et al. 2011). Conversely, species with concave curves (also referred to as concave up; Godfray 2011, Gabriel et al. 2013) can cope better with agriculture, and their populations are thus robust on low-intensity agricultural landscapes (we refer to these as sharing species, others call them loser or land-sharing species; Godfray 2011, Phalan et al. 2011). To translate this theory to practice, researchers typically estimate yield–density curves for many species, allowing species to be characterized as sharing, sparing, or intermediate (if the yield–density curve is neither convex nor concave). Counting the number of species in each category is then often thought of as a useful indicator for deciding on the choice of land management strategy; that is, either land sparing or land sharing (Phalan et al. 2011).

This approach differs greatly from conservation planning in other settings, where the goal is often to maintain a minimum population (or habitat area) for all species of conservation concern and where rigorous modeling techniques are commonly used to assess the benefits and trade-offs associated with alternative strategies (Margules and Pressey 2000, Carwardine et al. 2009, Moilanen and Arponen 2011). We propose that the approach of counting how many species are in each category, which underlies the land-sparing vs. land-sharing debate, does not translate well to landscape-scale maximization of overall richness of targeted species because (1) the number of species in each category is often not a useful indicator of how a landscape should be managed in order to minimize trade-offs between agricultural production and biodiversity. This is because in the common case, where intermediate species are present, neither a pure sparing or pure sharing landscape will be optimal, and if only sparing and sharing species are in the landscape, sparing landscapes are optimal, regardless of the relative number of species in each category. (2) Choosing a landscape management strategy based on the number of species in each category does not guarantee the survival of populations of all species of concern in a given landscape. We suggest that these weaknesses in how the land-sharing vs. land-sparing framework has been implemented to date can be mitigated by coupling the rich information entailed in the yield–density curves with optimization techniques in order to find truly
optimal solutions to aligning biodiversity conservation and agricultural production.

To illustrate these points, we propose a well-known optimization framework that maximizes agricultural production while satisfying population targets for any number of species. Next, we use simulated data to demonstrate how this optimization framework can be used to identify landscapes that maximize agricultural production while preserving species with varying yield-density curves. In this process, we show how the number of sparing, sharing, and intermediate species is generally a poor indicator of how a landscape should be managed. Finally, we show how optimization methods can identify landscapes that keep more species above a given population target than land-sparing or land-sharing strategies.

**METHODS**

A framework to maximize agricultural production while minimizing species loss

As currently framed, the land-sharing vs. land-sparing debate has centered on finding solutions which benefit most species. Here, we propose a framework for aligning agricultural production and biodiversity that minimizes species loss. We start with the idea that a landscape is made up of a number of parcels (or management units, grid-cells), and the goal of landscape management is to maximize the agricultural production of these parcels while maintaining a target population of each species of concern. Mathematically, this can be expressed as a constrained optimization problem

$$\max P \sum_{i=1}^{n} f(y_i, a_i) \text{ such that for all } c \text{ from } c = 1 : m,$$

$$S_c = \sum_{i=1}^{n} s_{ic} = f(y_{ic}, a_{ic}) \geq t_c$$

where $P$ is the total level of production on the landscape and is a function of the yield $y$ of parcel $i$ and its area $a$. There are $m$ species $c$ on the landscape and $S$ is the landscape-level population, such that $s_{ic}$ is equal to the population of species $c$ on parcel $i$. Importantly, $s_{ic}$ is also a function of yield and parcel size. The summation of parcel-level populations is equal to the total population of $c$ on the landscape $S_i$, and $t_c$ is the population target of species $c$. In the case of a no species loss policy, $t_c$ would be greater than zero for all $c$. The exact functional form of $s_{ic} = f(x_i, a_i)$ for each species is its yield-density curve, and determines how the population of each species changes with respect to yield.

Many land sparing/sharing studies (Phalan et al. 2011, 2014) focus on a production target rather than production maximization. Our framework can be easily adjusted to maximize species populations given a production target. To do so, one can simply change the maximized function from the production function to the yield-density functions and add an additional constraint that $P = w$, where $w$ is a production target for the landscape. With this framework, one can maximize the total population of all species on the landscape, while maintaining a target for each species, as well as an agricultural production target.

**Operationalizing the constrained optimization framework**

We solve the optimization model to highlight some of its general properties. To simplify interpretations, we first scale yields for each parcel between 0 and 1, with 1 being the maximum yield per unit. Likewise, we can scale $S_c$ such that the maximum population of any species on the landscape is equal to 1. This way, the population target can be interpreted as the percentage of the maximum population of a given species on the landscape.

The population of a given species on a given parcel ($s_{ic}$) is determined by the function

$$s_{ic} = 1 - \frac{y_{ic}}{\gamma_{ic}} + \gamma_{ic} - \gamma$$

where $\gamma$ is greater than 0 and determines whether a species has a convex (if $\gamma$ is between 0 and 1) or concave (if $\gamma$ is greater than 1) yield-density curve, $\gamma$ is an indicator variable and is equal to 0 for all species with convex or concave yield-density curves and 1 for the species that have an intermediate density yield curve, and $\gamma$ is greater than 1 and determines the shape of intermediate functions. Therefore, for species that are either land sharing or land sparing, $s_{ic}$ reduces to $1 - \frac{y_{ic}}{\gamma_{ic}}$.

We solved for the optimal yield for each parcel on the landscape given different suites of species and different population targets using the Matlab (MathWorks, Natick, Massachusetts, USA) optimization toolbox and original code (provided in the Supplement). We use a landscape with 100 parcels and nine species of concern. We ran the optimizations with five different species assemblages; (1) nine sharing species, (2) nine sparing species, (3) eight sharing and one sparing species, (4) one sharing and eight sparing species, and (5) three sparing, three sharing, and three intermediate species (Fig. 2). For each species assemblage, we solved for the optimal yield for each parcel, at species population targets ranging from 10% to 90%. After each optimization, we report graphically the yield of each parcel on the landscape.

To demonstrate the gains of using an optimization approach, we maximize species populations for assemblage 5 over five different production targets; 50%, 70%, 75%, 80%, and 85% of the maximum landscape yield. For each production target, we set a population target for each species of 10% of the maximum population. We then compare the number of species remaining above the species target across the optimal, land-sharing, and land-sparing landscapes.
RESULTS

Our optimization models reproduced the two ends of the land-sparing vs. land-sharing continuum. When all species had land-sharing yield–density curves, the full landscape was used, but yield per parcel was reduced as the species targets increased. When all species had land-sparing yield–density curves, yield was high on all the parcels that were used, but many parcels were not used at all (i.e., spared), and this number increased as the species target increased (Figs. 2 and 3).

Interestingly, for species assemblages that contained both sparing and sharing species (assemblages 3 and 4), optimal landscapes were identical to the optimization results for species assemblage 2 (i.e., only consisting of sparing species; Figs. 2 and 3). This is because for all intensity levels, the concave function had a higher population than the convex function and hence any solution which satisfied the convex function also satisfied the constraint of the concave function. Therefore, the convex function completely dictated the optimization problem, and we found that for any landscape with a mix of sparing and sharing species, a land-sparing solution will be optimal (at least for the functional forms used here). The number of species in each category did not matter.

When sharing, sparing, and intermediate species were all present in the landscape, the optimal solution was a mix of land-sparing and land-sharing strategies. Some parcels were always spared, but parcels that were used were generally not used at maximum yield. Overall then, when all three forms of density yield curves were present, the optimal solution combined characteristics from both land-sharing and land-sparing landscapes (Figs. 2 and 3).

We used a production target approach to identify the gains from optimization. In order to do so, we solved a model using assemblage 5 and a population target of 10%, for production targets ranging from 50% to 85% of the maximum yield. When the land-sharing strategy (i.e., the production target was met by having the lowest possible yield spread across the full landscape) was used, all nine species met their population target at the 50% production target, however, this number decreased to six out of nine species when the production target was 85%. The three species which did not meet the 10% population target were the three land-sparing species, which require nearly natural landscapes without land use to maintain populations. Using the land-sparing strategy (i.e., the production target was met using the minimum amount of land for production), seven species met the population target regardless of the production target, however, this number decreased to six out of nine species when the production target was 85%. The three species which did not meet the 10% population target were the three land-sparing species, which require nearly natural landscapes without land use to maintain populations. Finally, when the optimization strategy was used, all nine species were able to meet the population target for each production target (Fig. 4).

<table>
<thead>
<tr>
<th>Species assemblage</th>
<th>Description</th>
<th>Yield density curves</th>
<th>Landscapes that maximize production with all species maintained at 50% of maximum population</th>
</tr>
</thead>
<tbody>
<tr>
<td>1</td>
<td>All nine species are sharing</td>
<td><img src="image1" alt="Image" /></td>
<td><img src="image2" alt="Image" /> 50% yield</td>
</tr>
<tr>
<td>2</td>
<td>All nine species are sparing</td>
<td><img src="image3" alt="Image" /></td>
<td><img src="image4" alt="Image" /> 0% yield 100% yield</td>
</tr>
<tr>
<td>3</td>
<td>Eight species are sharing, one species is sparing</td>
<td><img src="image5" alt="Image" /></td>
<td><img src="image6" alt="Image" /> 0% yield 100% yield</td>
</tr>
<tr>
<td>4</td>
<td>One species is sharing, eight species are sparing</td>
<td><img src="image7" alt="Image" /></td>
<td><img src="image8" alt="Image" /> 0% yield 100% yield</td>
</tr>
<tr>
<td>5</td>
<td>Three species are sharing, three are sparing, and three are intermediate</td>
<td><img src="image9" alt="Image" /></td>
<td><img src="image10" alt="Image" /> 0% yield 50% yield 80% yield</td>
</tr>
</tbody>
</table>

Fig. 2. Optimization framework modeled over five different species assemblages. The results are from the maximization over 100 parcels; here we summarize these results over 20 parcels for expositional purposes.
DISCUSSION

Balancing agricultural production and biodiversity conservation is a daunting challenge. The land-sparing vs. land-sharing debate has provided important insights into this issue and stimulated useful debate around trade-offs between agriculture and conservation (Balmford et al. 2005, Green et al. 2005, Perfecto and Vandermeer 2010, Phalan et al. 2011). At the same time, room for improvement in how this debate is framed, particularly because it disregards important issues of food security and sovereignty, (Fischer et al. 2014), and how quantitative models are used, for example due to the unsatisfactory treatment of environmental heterogeneity, displacement, and scaling effects (Grau et al. 2013), have become apparent.

![Graphs showing species assemblages](image)

**Fig. 3.** Results of optimization program for species assemblages (Fig. 2). The results of the optimization for assemblage 1 show that each parcel is used (i.e., each of the 100 colors can be seen) and the yield per parcel decreases as the species population target increases. This is the classic land-sharing result; no land is spared for nature, and the yield on each parcel is less than its potential maximum. For assemblage 2, the number of used parcels decreases as the population target increases (i.e., the number of colors decrease as more parcels are spared), but the yield of the parcels that are used is always at the maximum. This is a classic land-sparing landscape. We found identical results for assemblages 3 and 4. For assemblage 5, we see that the yield is not at the maximum, and some land is spared. Therefore, when all types of species yield curves are on the landscape, we see a combination of land-sharing and land-sparing strategies is optimal. We note that there is no feasible solution for population targets over 80%.

**Fig. 4.** Number of species above the population target of 10% for various production targets (50–85% of maximum yield) and species assemblage 5. We calculate the number of species above the population target for an optimized landscape, a land-sharing landscape, and a land-sparing landscape. In the land-sharing landscape, we can preserve all species while producing 50% of the maximum yield. However, as yield increases, the number of species above our target level decreases, to the point where only six species remain above the 10% target when yield is equal to 85% of the maximum. In this case, the sharing and intermediate species are maintained but the sparing species fall below the threshold. When the land-sharing approach is applied, both the sharing and sparing species meet the population target in for each yield target. However, two of the three intermediate species do not meet the 10% target. This is because the land-sharing strategy leaves no land in intermediate use, and therefore the intermediate species are never above the population target. Using the optimization method, all nine species are able to meet the population target at each production target.
Most quantitative studies applying the framework so far have assessed species’ responses to the two contrasting land-use strategies of sparing and sharing, and imply that landscape-level management should utilize the strategy that would benefit the most species. Here, we show that such a black-and-white approach will inevitably lead to less-than-optimal solutions in situations where a landscape contains species with diverse yield-density curves. In particular, we assert that a modeling framework for aligning agricultural production and biodiversity conservation goals should (1) not emphasize the number of species in each category, and (2) be capable of ensuring the survival of all species of conservation concern at the scale of the analysis, acknowledging that choosing the right scale for analysis is difficult (Margules and Pressey 2000). To meet these goals, we suggest that the rich information present in yield-density curves be combined with optimization techniques in order to identify landscapes that align agricultural production and biodiversity goals.

Our results suggest that the relative number of sharing and sparing species is not a useful indicator of how the landscape as a whole should be managed. If both sparing and sharing species are present, then land-sparing solutions are the best, regardless of the relative number of species in each class, at least for the functional forms of the yield–density curves used here. In cases where intermediate species are present, the optimal solution is a combination of land sharing and sparing. This suggests that solutions which have features of both strategies may be optimal in many real-world landscapes where diverse yield-density curves are the norm (Phalan et al. 2011), especially in regions with long land-use histories where agrobiodiversity may depend on low-intensity land use (Jackson et al. 2007, Fischer et al. 2012, Ekroos et al. 2014). This result has been predicted by a host of authors who have argued that in real-world landscapes, a combination of both sharing and sparing strategies is likely needed (Phalan et al. 2011, Tscharntke et al. 2012, Ramankutty and Rhemtulla 2013). Our results can thus be seen as a theoretical example supporting this assertion.

While adopting a simple landscape management strategy based on the number of species with particular yield-density curves may lead to suboptimal outcomes, switching to a more nuanced optimization framework is a straightforward step. Optimization techniques have been used to model trade-offs in the past (Polasky et al. 2008, Nelson et al. 2009, Pouzols and Moilanen 2013), and have been the workhorse for economic modeling for generations (Chiang 1984). The most resource-consuming part of optimization models is likely data collection to estimate the yield–density curves. Yet these yield–density curves have not been explored to their maximum potential in the context of land-sparing vs. land-sharing applications. By using the full information in them, one can find more nuanced and context-dependent solutions to mitigate agriculture–biodiversity trade-offs. This is an important step forward from debates centered on choosing between idealized and extreme land management paradigms such as sparing or sharing, both of which can result in undesired outcomes.

Like any model, ours too has its limitations. First, our model does not include measures of landscape connectivity or fragmentation, both of which can be important in determining species’ survival (Fahrig 2003, Pardini et al. 2010). Second, as in other nonspatial optimization frameworks, our model does not consider spatial heterogeneity in yields or biodiversity (e.g., species turnover). Third, our model is partial equilibrium in nature. Therefore, we are only concerned about optimization over the extent of the area used in the model. As even distant areas can be linked (e.g., via trade or animal migrations), optimal solutions identified for one region may not hold when linkages to other regions are considered (Polasky et al. 2004). Yet our model does not currently consider such connections that would be key to addressing multi-scale optimization problems. Relaxing these constraints in the model is an area ripe for future research.

The overarching goal of many researchers and practitioners engaged in agriculture/biodiversity research is to find pathways to land systems where biodiversity is maintained and food can be produced in abundance. Quantitative assessments of whether land-sparing or land-sharing paradigms are superior in doing so has sparked much insightful debate, but also highlighted shortcomings of the current set of models (Grau et al. 2013, Fischer et al. 2014). We show that a decision support system that forces managers to choose one of the contrasting alternatives of sparing or sharing may result in suboptimal outcomes. The optimization framework we present here allows us to move away from such broad black-and-white choices and thus to identify landscapes which maximize the provision of both food and biodiversity. Interestingly, our quantitative modeling results add to and enforce a number of conceptual remarks calling for a more nuanced, context-specific view on agriculture–biodiversity trade-offs. We suggest that there is great power in combining yield-density curves with optimization tools and that expanding this line of research may be a fruitful way for researchers to help align food production and biodiversity conservation goals.

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