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Analytical Solutions to Trade-Offs between Size of Protected Areas and Land-Use Intensity

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Abstract: *Land-use change is affecting Earth's capacity to support both wild species and a growing human population. The question is how best to manage landscapes for both species conservation and economic output. If large areas are protected to conserve species richness, then the unprotected areas must be used more intensively. Likewise, low-intensity use leaves less area protected but may allow wild species to persist in areas that are used for market purposes. This dilemma is present in policy debates on agriculture, housing, and forestry. Our goal was to develop a theoretical model to evaluate which land-use strategy maximizes economic output while maintaining species richness. Our theoretical model extends previous analytical models by allowing land-use intensity on unprotected land to influence species richness in protected areas. We devised general models in which species richness (with modified species-area curves) and economic output (a Cobb–Douglas production function) are a function of land-use intensity and the proportion of land protected. Economic output increased as land-use intensity and extent increased, and species richness responded to increased intensity either negatively or following the intermediate disturbance hypothesis. We solved the model analytically to identify the combination of land-use intensity and protected area that provided the maximum amount of economic output, given a target level of species richness. The land-use strategy that maximized economic output while maintaining species richness depended jointly on the response of species richness to land-use intensity and protection and the effect of land use outside protected areas on species richness within protected areas. Regardless of the land-use strategy, species richness tended to respond to changing land-use intensity and extent in a highly nonlinear fashion.*

Keywords: analytical model, human-natural systems, land sharing, land sparing, species richness, sustainability, wildlife-friendly farming

Soluciones Analíticas a las Ventajas y Desventajas entre el Tamaño de Áreas Protegidas y la Intensidad del Uso de Suelo

Resumen: *El cambio en el uso de suelo esta afectando la capacidad de la Tierra para soportar tanto especies silvestres como una población humana creciente. La pregunta es como manejar los paisajes tanto para la conservación de especies como para fines económicos. Si grandes extensiones son protegidas para conservar la riqueza de especies, entonces las áreas no protegidas deben ser utilizadas más intensivamente. Asimismo, el uso de baja intensidad deja menos superficie protegida pero puede permitir que especies silvestres persistan en áreas que son utilizadas con fines de mercado. Este dilema esta presente en los debates sobre políticas agrícolas, de vivienda y forestales. Nuestra meta fue desarrollar un modelo teórico para evaluar que estrategia de uso de suelo maximiza el producto económico al tiempo que mantiene la riqueza de especies. Nuestro modelo teórico extiende modelos analíticos previos al permitir que la intensidad en el uso de suelo en tierras no protegidas influya sobre la riqueza de especies en tierras protegidas. Diseñamos modelos generales en los que la riqueza de especies (con curvas de especies-área modificadas) y el producto económico (una*

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función de producción Cobb–Douglas) son una función de la intensidad del uso de suelo y de la proporción de terreno protegido. El producto económico incrementó a medida que incrementaron la intensidad del uso de suelo y la proporción tierra protegida, y la riqueza de especies respondió al incremento de intensidad tanto negativamente como siguiendo la hipótesis de perturbación intermedia. Resolvimos el modelo analíticamente para identificar la combinación de intensidad en el uso de suelo y la superficie protegida que proporcionaron la cantidad máxima de producto económico, dado un nivel determinado de riqueza de especies. La estrategia de uso de suelo que maximizó el producto económico al tiempo que mantenía la riqueza de especies dependió conjuntamente de la respuesta de la riqueza de especies a la intensidad en el uso de suelo y protección y el efecto del uso de suelo afuera de las áreas protegidas sobre la riqueza de especies dentro de las áreas protegidas. Independientemente de la estrategia de uso de suelo, la riqueza de especies tendió a responder a cambios en la intensidad y extensión del uso de suelo en una manera altamente no lineal.

Palabras Clave: agricultura amistosa con la vida silvestre, modelo analítico, riqueza de especies, sistemas humanos-naturales, sustentabilidad, tierras compartidas, tierras de reserva

Introduction

Protected areas are a cornerstone of efforts to conserve species. However, intensifying human land use surrounding protected areas reduces the ability of protected areas to conserve species (Hansen & DeFries 2007; Radeloff et al. 2010). In unprotected areas, species extinctions depend largely on how intensively humans use the land (e.g., agriculture or housing) and whether the uses lead to, for example, introduction of pathogens or invasive species (Benton et al. 2003; Jackson & Sax 2010).

Concurrently, rising global consumption of natural resources places increased demands on the Earth's ability to sustain the human species (Myers & Kent 2003). Increasing global consumption suggests that land-use expansion and intensification will continue to drive extirpations and extinctions via habitat loss and fragmentation and decreases in habitat quality (Sala et al. 2000). These effects threaten provision of ecosystem services (especially for services not traded in the market) and ultimately human well-being (Diaz et al. 2006; Dobson et al. 2006). Managing landscapes to optimize the trade-offs between market-based economic output and the protection of species has thus become one of the most pressing topics in conservation.

For a given piece of land, the most effective conservation strategy is typically to limit land-use intensity. The extreme form of such limits is a protected area with strong enforcement in which human disturbance is minimized. However, if humans expect the terrestrial surface of Earth to provide a certain level of commodities, then as the proportion of protected land increases, the remaining area must be used more intensively, and such use can (Mitrovich et al. 2010) have negative effects on species richness in unprotected areas.

Trade-offs between land-use intensity and extent have sparked debates about agricultural land use (sometimes referred to as the land-sparing versus land-sharing debate [Fischer et al. 2008; Clough et al. 2011; Phalan et al. 2011]) and conservation of species richness, or the land-sparing versus wildlife-friendly-farming debate (Green et al 2005; Matson & Vitousek 2006; Vandermeer & Perfecto 2007). This debate is not unique to agricultural land use. In the case of housing development the debate is about large lots sizes versus clustering of housing units (Niell et al. 2007; Pejchar et al. 2007; Gagne & Fahrig 2010), and in forestry the debate is about whether to conduct clearcuts over relatively small areas or selective harvests over relatively large areas (Cote et al. 2009).

Effects of land-use intensity on species richness differ among taxonomic groups and land uses (Tews et al. 2004; Alberti 2005), but usually species richness decreases monotonically as land-use intensity increases or species richness increases initially as land-use intensity increases and then decreases as intensity continues to increase. Nonlinear responses of species richness to land-use intensity have been identified for mammals (Wenguang et al. 2008; Panzacchi et al. 2010), fishes (Alberti 2005), birds (Blair 1999; Hansen et al. 2005; Lepczyk et al. 2008), and insects (Blair 1999; Gagne & Fahrig 2010). Increases in agricultural intensity usually result in decreases in species richness (Reidsma et al. 2006; Flynn et al. 2009; Fletcher et al. 2011), whereas increases in housing density may lead to a unimodal response in species richness (Pautasso & Dinette 2009).

The effect of land-use intensity outside protected areas on species richness inside protected areas also varies. Generally, as protected area size increases, the effect of outside land use intensity on species richness exerts less effect on species richness. However, the more intensive the land-use surrounding a given protected area, the greater the decrease in functional size and ecological flows (Hansen & Rotella 2002; Vester et al. 2007). Finally, increased land-use intensity outside a protected area may have nonlinear effects on species richness within protected areas (Carroll et al. 2003).

In conservation biology, trade-offs between extent of protected areas and land-use intensity are usually framed as a trade-off between conserving species and producing enough goods to sustain human populations (Green et al. 2005; Perfecto & Vandermeer 2010). Alternatively, economic models of land use commonly frame the trade-off as maximization of profit by individual landowners facing regulatory or capital constraints (Barbier 2007; Takasaki 2007). Here, we assumed a societal goal of maximizing output to provide for a consistently increasing global population size and that regulations require the conservation of a specific number of species. Given these assumptions, we examined levels of land-use intensity and amounts of protected area that provide maximum economic output while conserving a target level of species richness given a range of responses of species richness to land-use intensity and varied effects of land-use intensity outside protected areas on species richness within protected areas.

We extended past analytical approaches (Green et al. 2005) in 2 distinct ways. First, we assumed land use outside protected areas affects species richness inside protected areas. Second, we not only solve for the mathematically optimum solution, but we also determined all the trade-off combinations among economic output, protected area size, and species richness. We address 4 questions. First, how does changing land-use intensity and proportion of the landscape protected affect species richness given alternative functional relations between land use and species richness? Second, assuming changes in species richness are mainly a function of changes in land-use intensity at community to landscape scales, what percentage of the landscape must be protected to assure maintenance of a specific target of species richness for varying levels of land-use intensity? Third, what are the trade-offs between species richness and economic output? Fourth, does low-intensity land use over an extensive area or high-intensity land use over a small area maximize economic output while maintaining a target level of species richness?

Methods

Species-Richness Model

We developed a model of species richness that accounts for heterogeneous responses of species richness to land-use intensity (S_o) and responses of species richness inside protected areas to land use outside protected areas (S_i). We modeled S_o in 2 functional forms: a stress response (Eq. 1) in which species richness outside the protected area decreased linearly as land-use intensity increased, and an intermediate response (Eq. 2) in which species richness increased when land-use intensity was low, but decreased below the original species richness when land-use intensity was high

$$S_{o\text{stress}} = (1 - d \times q) \tag{1}$$

and

$$S_{o\text{intermediate}} = (1 - d) + x^2 \times d - (x \times d)^2 , \tag{2}$$

respectively, where d is land-use intensity ($0 \leq d \leq 1$) and q and x are constants.

We modeled S_i in 3 functional forms: an independent response (Eq. 3) in which species richness inside the protected area was not affected by land-use intensity outside, a stress response (Eq. 4) in which species richness inside the protected area decreased as land-use intensity outside increased, and a threshold response (Eq. 5) in which species richness inside the protected area was affected only by land-use intensity outside the protected area above a certain threshold

$$S_{i\text{independent}} = 1, \tag{3}$$

$$S_{i\text{stress}} = 1 - [(1 - r) \times d] , \tag{4}$$

and

$$S_{i\text{threshold}} = J \times [(1 - d) + x^2 \times d - (x \times d)^2], \tag{5}$$

respectively, where the indicator function $J = 1$ if $(1 - d) + x^2 \times d - (x \times d)^2 < 1$; otherwise, $J = 0$.

We assumed a homogenous landscape of arbitrary size and species richness. Because the landscape was homogenous, we did not calculate beta or gamma diversity. We scaled species richness from 0 to 1, where 1 represented the number of species on the landscape when there was no human land use. The total landscape area equaled 1. If a protected area was established, it covered a proportion of the landscape ($0 \leq r \leq 1$) ($1-r$ was outside of the protected area; we did not consider the spatial configuration of the protected area or network of protected areas), and we assumed land-use intensity inside the protected equaled 0. Using a modification of the classic species-area curve (i.e., $S = cA^z$ [MacArthur & Wilson 1967]), we calculated the percentage of species in the protected area as r^z, where z is between 0 and 1 and dictates the shape of the species-area curve. The main modification we made to the species area curve was to drop the scalar c, which affected the number of species, but not the percentage of species present on the landscape. Assuming there was no human use of land outside the protected area, the percentage of species located only outside the protected area was $1 - r^z$. Total species richness was thus the percentage of species inside the protected area (r^z) plus the percentage of species only outside the protected area ($1 - r^z$) and equaled 1 when land-use intensity equaled 0 (Fig. 1).

Thus, species richness as a percentage of total species richness (SR) can be written as

$$\text{SR} = r^z \times S_i + \left(1 - r^z\right) \times S_o. \tag{6}$$

We produced 4 models of responses of species richness to land-use intensity and the portion of the landscape that is in protected areas (Fig. 2): independent response inside the protected area and stress response outside (independent–stress); independent

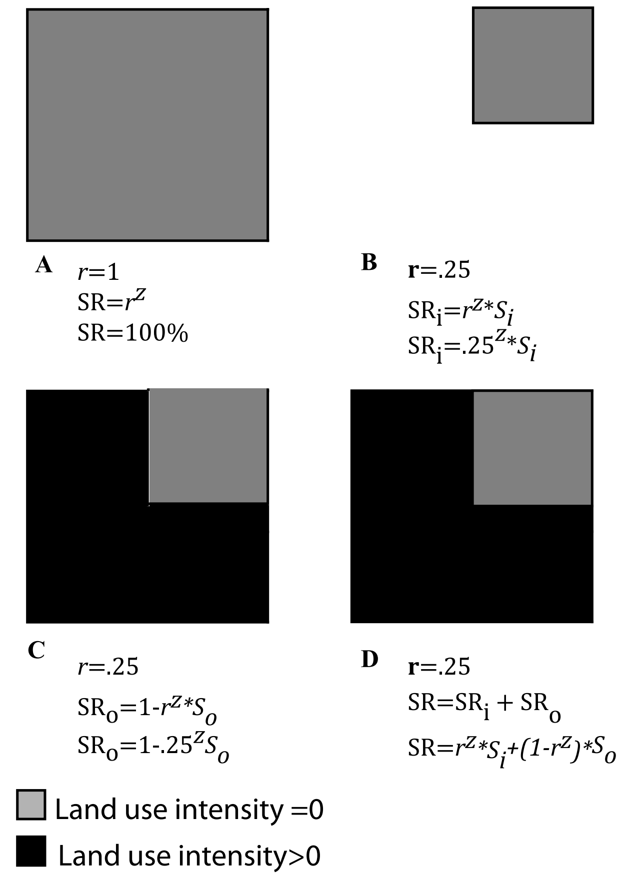

Figure 1. Calculations of species richness in a landscape with protected and unprotected areas: (a) landscape of arbitrary size with zero human land use, where species richness is 100% of total species, (b) 25% of the landscape is protected and the proportion of landscape-level species richness within the protected area is 0.25^z*, (c) the number of unique species outside the protected area is* $1 - 0.25^z$*, (d) 25% of landscape is protected and 75% is unprotected and land-use intensity is* >0 *(SR, species richness;* SR_o*, species richness outside protected areas;* SR_i*, species richness inside protected areas; r, percentage of landscape protected; d, intensity of land use; z, slope of species area relation in log-log space; t, target percentage of species to conserve; q, model constant; x, model constant;* S_i*, relation between species richness and land-use intensity inside the protected area;* S_o*, relation between species richness and land-use intensity outside the protected area).*

response inside and intermediate response outside (independent–intermediate); stress response inside and outside (stress–stress); and threshold response inside and intermediate response outside (threshold–intermediate).

Economic-Output Model

We used a simple economic output model in which the economic output of a landscape was a function of land-use intensity (d) and extent ($1 - r$) and increased in intensity and extent as economic output increased. Economic output range was 0–1 and was 1 when intensity and extent each equaled 1 (i.e., there were no protected areas and land-use intensity was at a maximum).

We modeled economic output with a variation on the Cobb–Douglas production function. We replaced the normal inputs to production, capital, and labor with land-use intensity (d) and extent ($1 - r$). Increases in both land-use intensity and extent always increased output, but economic output per unit increase in intensity and extent decreased as intensity and extent approached 1. The parameter $\gamma (0 \le \gamma \le 1)$ was the output elasticity of land-use intensity and $1 - \gamma$ was the output elasticity of extent. We assumed the output elasticity of intensity and extent were equal (i.e., $= 0.5$) such that increasing intensity and extent proportionately increased production. As such,

$$\mathrm{EO} = d^{\gamma}\,(1 - r)^{1-\gamma}\,. \tag{7}$$

We did not apply this model as it is usually applied in neoclassical economics. Typically, a production function is paired with a cost function that is then used to find profit-maximizing solutions. Instead, we were interested in solutions that potentially maximize output—as opposed to profit. Hence, we did not include a cost function and thus assumed there was no cost constraint. Our solutions maximized output, but they were not efficient in the economic sense of profit maximization. Because we did not base the model on profit maximization, we did not assume the solutions we found were the result of individual actors acting rationally. Rather, we assumed the solutions were optimal if society's goals were to maximize output given a species-richness constraint.

Combined Species Richness and Economic Output Models

We calculated how species richness changed as a function of changes in protected area size and land-use intensity by taking first and second derivatives of the species-richness models with respect to protected area size and land-use intensity. Given the assumed parameters of the model, the sign of the derivatives could be negative, positive, or inconsistent (i.e., the sign of the derivative changes depending on the values of the model parameters). The sign of each derivative was the effect on species richness of increasing either the percentage of area protected or land-use intensity. We calculated the maximum land-use intensity for each possible size of protected area (at intervals of 0.001) for a given target of species richness—in our case 95% of the total number of species. At any point along the curve, decreasing protected area size or increasing intensity resulted in the

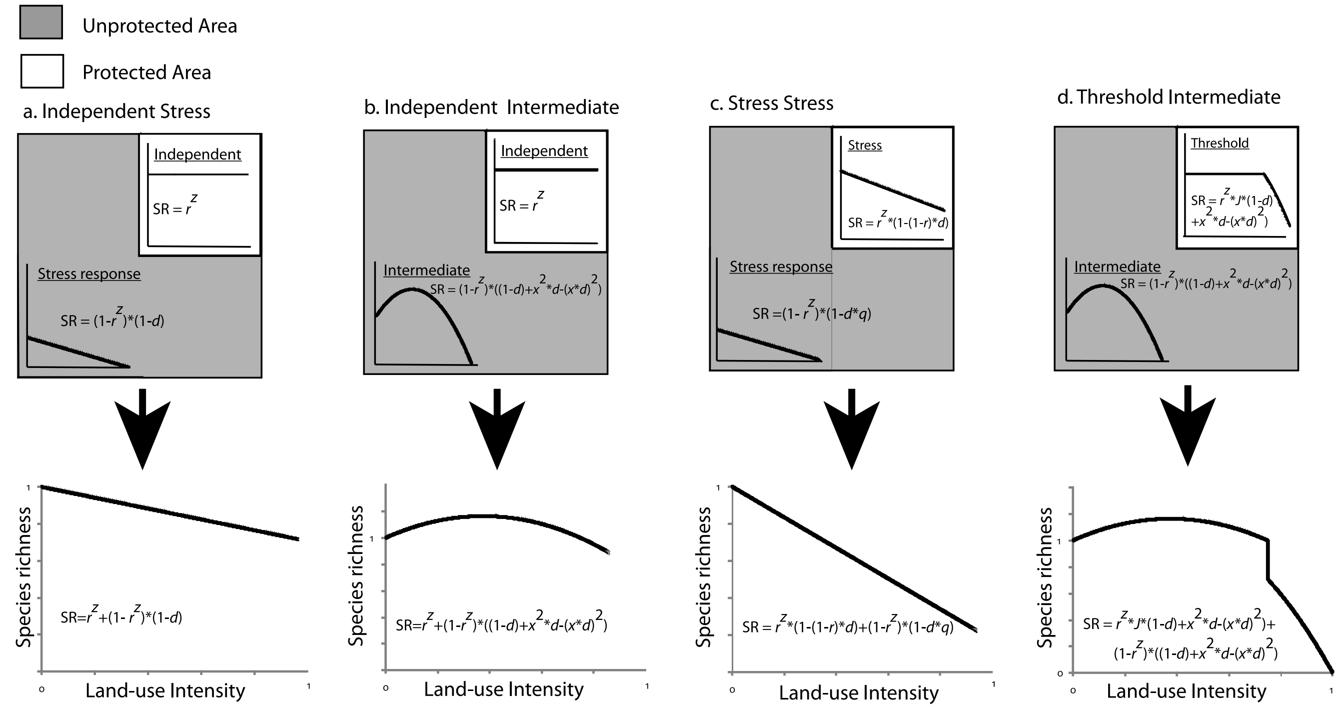

Figure 2. Effect of land-use intensity on species richness (SR) inside and outside protected areas: (a) independent-stress response, $\mathrm{SR} = r^z + (1 - r^z) \times (1 - d)$*; (b) independent-intermediate response,* $\mathrm{SR} = r^z + (1 - r^z) \times [(1 - d) + x^2 \times d - (x \times d)^2]$*; (c) stress-stress response,* $\mathrm{SR} = r^z \times [1 - (1 - r) \times d] + (1 - r^z) \times (1 - d \times q)$*; (d) threshold-intermediate response* $\mathrm{SR} = r^z \times J \times [(1 - d) + x^2 \times d - (x \times d)^2] + (1 - r^z) \times [(1 - d) + x^2 \times d - (x \times d)^2]$*. Graphs in the top row show response of species richness to land-use intensity inside (top right graphs) and outside (bottom left graphs) of protected areas. Graphs in the bottom row show the responses of species richness to land-use intensity inside and outside protected areas combined. Equation variables are defined in Table 1.*

target of species richness not being met. The points on the resulting curve can thus be considered points where land-use intensity is at a maximum and the target level of species richness is maintained.

We used both the economic and species-richness models to calculate the functional relation between species richness and economic output by calculating the maximum species richness at a given level of economic output. The resulting curves represented the maximum species richness that could be attained for a given economic output. For each possible level of economic output, we calculated the maximum possible value of species richness.

Finally, to identify the values of percentage of protected area and land-use intensity that maximize economic output given a target species richness, we solved the following for each species richness model:

$$\max \quad \mathrm{EO}(d, r) \tag{8}$$

$(s.t.\ \mathrm{SR} = t)$, where t is the target species richness (i.e., the total percentage of species to be protected).

Results

In both the independent-stress and stress-stress models species richness increased when the percentage of land protected increased. In the independent-intermediate and threshold-intermediate models, increasing the proportion of protected area was not always associated with an increase in species richness. Increasing size of protected area was associated with a decrease in species richness if species richness responded to land-use intensification according to the intermediate-disturbance hypothesis. Similarly, when land-use intensity increased, species richness increased initially before decreasing at higher land-use intensities (Table 1 & Figs. 3a & b).

The relation between percentage of area protected and land-use intensity while maintaining 95% of species

Table 1. Signs of first derivatives (second derivatives not shown) of the species richness model with respect to protected area size and land-use intensity.

Species richness model	$\frac{\partial SR}{r}$	*Sign of derivative*	$\frac{\partial SR}{r}$	*Sign of derivative*
Independent-stress	$\frac{r^z z}{r} - \frac{r^z z(1-d)}{r}$	positive	$-1 - r^z$	negative
Independent-intermediate	$\frac{r^z z}{r} - \frac{r^z(1-d+x^2d-d^2x^2)}{r}$	dependent on parameters	$(1-r^z)(-1+x^2-2x^2d)$	dependent on parameters
Stress–stress	$\frac{r^z z\{1-[(1-r)d]\}}{r} + r^z d - \frac{r^z z(1-d)}{r}$	positive	$r^z(-1+r) - 1 + r^z$	negative
Threshold-intermediate	$\frac{r^z(1-d+x^2d-d^2x)^2}{r} - \frac{r^z\left(1-d+x^2d-d^2x^2\right)}{r}$	dependent on parameters	$2r^z(1-d+x^2d-dx)$ $(-1+x^2-x)$ $+(1-r^z)(-1+x^2-2x^2d)$	dependent on parameters

Note: *Variables: SR, species richness; r, percent of landscape protected; d, intensity of land use; z, slope of species area relation in log-log space; x, model constant.*

richness was nonlinear. At points above the curves (Figs. 3c & d), the maintaining of 95% of species richness was met by protecting less area or increasing land-use intensity. At points below the curve, the species-richness target was not met. In all 4 models, when land-use intensity was low, 95% of species richness could be maintained without protecting any land (Figs. 3c & d). The intensity of land-use before species richness declined varied from model to model and within models as a function of the values for z, q, and x. In all our models, at certain points along the curve, even a small increase in land-use intensity dramatically increased the percentage of

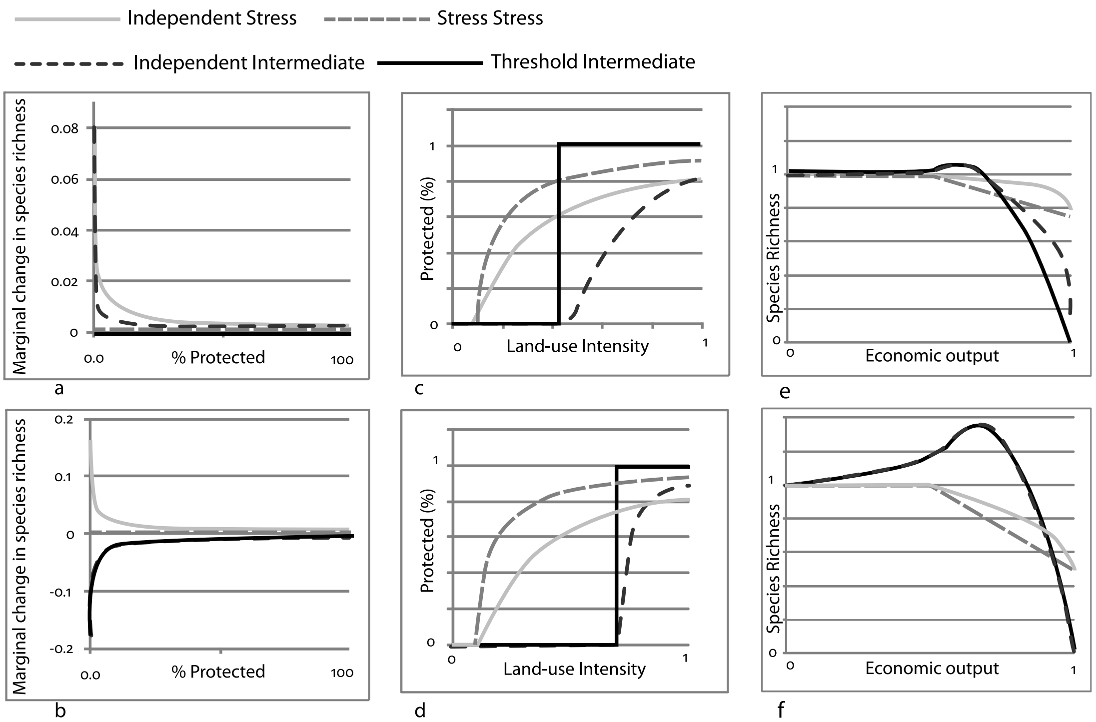

Figure 3. Marginal change in percent total species richness for a 1% increase in protected area when land-use intensity is held constant ([a] land-use intensity 25% and [b] land-use intensity 10%);(c, d) efficient combinations of protected area and land-use intensity (x-axis) when species richness is held constant at 95% for alternative parameters; and (e, f) maximum species richness and economic values for alternative parameters. In (a), (c), and (e), $z = 0.25$, $x = 1.25$, and $q = 0.5$, *respectively, and in (b), (d), and (f),* $z = 0.25$, $x = 1.75$, and $q = 1.0$, *respectively* (z, *slope of species area relation in log-log space;* q, *model constant;* x, *model constant).*

Table 2. Values of land-use intensity and percentage of land protected that maximizes economic output given a species richness constraint.

Species richness model	*Optimal land-use intensity (i.e., value of* d)	*Optimal land protected (%)*
Independent-stress	1	$e^\wedge\left(\frac{\ln t}{z}\right)$
Independent-intermediate	$0 < d < 1$	$0 < r < 1$
Stress-stress	$(1 - t)/q$	0
Threshold-intermediate	$\frac{-1 + x^2 + \sqrt{1 + 2x^2 + x^4 - 4x^2 t}}{2x^2}$	0

Note: *Variables: r, percentage of landscape protected; d, intensity of land use; z, slope of species area relation in log-log space; t, target percentage of species to conserve; q, model constant; x, model constant.*

protected area necessary to satisfy the species-richness target.

The relation between species richness and economic output was also nonlinear. At points along the curve for species richness and economic output (Figs. 3e & f), species richness could not increase without decreasing economic output or vice versa. At points under the curve, higher species richness or higher economic output was possible. In all models, nearly all targets of species richness could be maintained in tandem with about 25% of economic output, although the exact value of economic output depended highly on the parameters of the model. In all models, species richness decreased as economic value approached 1.

An analytical proof of the maximum economic output for each species richness land-use relationship is available in Supporting Information. For the independent-stress model, the maximum economic output occurred when land use was most intense and when percentage of protected area was at the minimum needed to maintain the target percentage of species richness, $r = e^\wedge(\frac{\ln t}{z})$. For the stress-stress model, economic output was maximized when no area was protected and land-use intensity was equal to $(1 - t)/q$. The threshold-intermediate model had a similar result. Economic output was maximized when no area was protected and land-use intensity was equal: $\frac{-1+x^2+\sqrt{1+2x^2+x^4-4x^2 t}}{2x^2}$. No analytical solution existed for the independent-intermediate model that maximized economic output while maintaining species richness; both r and d had to be >0 and <1. Thus, the landscape that maximized economic output while maintaining a target species richness was a mix of protected and unprotected land (Table 2 and Fig. 4) (see Supporting Information for more details).

Discussion

Our goal was to provide a theoretical answer to whether the goals of maintaining species richness and economic output are best achieved by protecting large areas and using other areas at high intensity or by protecting small areas and using other areas at low intensity. Our analyses extended past analytical results (Green et al. 2005) by addressing multiple responses of species richness to

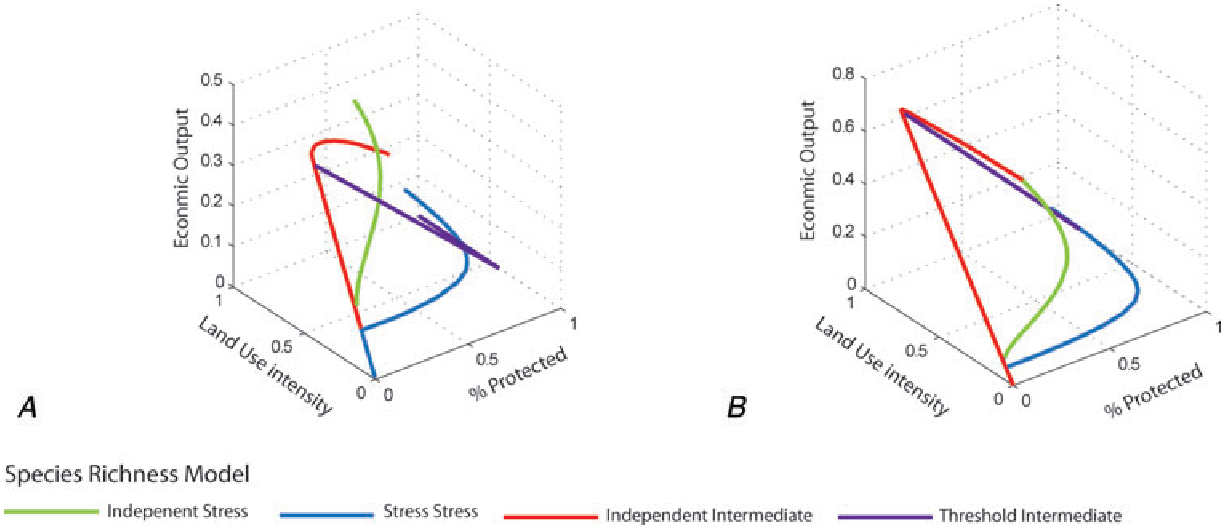

Figure 4. Protected area and land-use intensity that satisfy the species richness target of 95% for alternative parameters: (a) $z = 0.25$, $x = 1.25$, and $q = 0.5$ *and (b)* $z = 0.25$, $x = 1.75$, and $q = 1.0$ *(z, slope of species area relation in log-log space; q, model constant; x, model constant).*

land-use intensity and because we assumed land use outside protected areas affects species richness inside protected areas. Likewise, we modeled curves of the response of species richness to multiple levels of economic output. There were no single optimal values of percent protected area and land-use intensity, even in this relatively simple model. Our results, therefore, support views that there are no universal solutions to resource-use problems in complex social and ecological systems (Ostrom et al. 2007; Brock & Carpenter 2008) and that the land-use debate should not be framed as a black and white choice.

In our models, the optimal values of percent protected area and land-use intensity depended on the assumed relations between land-use intensity and species richness. When we assumed land use outside protected areas did not affect species richness inside protected areas and that species richness decreased as land-use intensity increased (e.g., the independent–stress model), it was optimal to protect large areas and use other areas at high intensity (Balmford et al. 2005; Green et al. 2005; Aratrakorn et al. 2006). However, when we instead assumed species richness had a unimodal response to land-use intensity, the optimal landscape required both protected and unprotected areas. When we assumed that land use outside protected areas affected species richness inside protected areas, then it was optimal to protect no land and to use land at low intensity, regardless of the response of species richness outside protected areas (stress–stress and threshold–intermediate models). This result, therefore, is consistent with the idea of species conservation on unprotected land (Vandermeer & Perfecto 2007; Clough et al. 2011).

Our results are not consistent with those of some previous studies (Green et al. 2005; Gagne & Fahrig 2010; Phalan et al. 2011) that show large protected areas and high-intensity land use is the optimal solution when it is not assumed that land use outside protected areas and species richness in protected areas interact. We found that when we included an interaction in which increasing intensity of land use outside protected areas affected species richness in protected areas, large protected areas and high-intensity land use was never the solution. This result held even when we assumed a homogenous landscape, which has been considered the ideal case for large protected areas and high-intensity land use on remaining unprotected land (Fischer et al. 2008). Land use outside protected areas affects species in protected areas, even in protected areas that are relatively separated from intense human activity (Waggoner 1996; Haila 2002; Fischer et al. 2004). Thus, our results are consistent with prior findings that there are interactions between protected and unprotected areas that have a large effect on both biological diversity and economic output (Kremen et al. 2004; Ricketts 2004; Morandin & Wilson 2006).

In all our models, relations between economic output and species richness were nonlinear; small changes in one of the parameters (either area protected or intensity) often required large changes in the other to maintain species richness. Strong nonlinearities have been found in other models of dynamic social and ecological systems (Scheffer et al. 2001; Walker & Meyers 2004). Optimizing landscapes for either economic output or species conservation may reduce the resilience of species richness to economic output (Folke et al 2004; Liu et al. 2007), whether percent protected area and land-use intensity is low or high. In our models, threshold responses of species richness to economic output were more marked in the case of small protected areas and low-intensity land use.

Our approach and hence our results have limits. Most importantly, our assumption of a homogenous landscape limits our predictions to alpha diversity (i.e., species richness). If maximizing gamma diversity is not a product of maximizing alpha diversity on a landscape (i.e., as can be the case when the intermediate-disturbance hypothesis is used to calculate alpha diversity or on a heterogeneous landscape), our model results may differ from real-world conditions. Thus, our models are likely most informative for management of relatively heterogeneous landscapes, localized areas, and instances where alpha and gamma diversity are similar. Integrating heterogeneous landscapes as well as beta and gamma diversity into our theoretical approach is an important area for further research. We are also relatively uncertain about the robustness of solutions that suggest landscapes optimal for species richness contain no protected areas. Increases in species richness associated with increases in intensity of land use may be the result of colonization by non-native species (Gavier-Pizarro et al. 2010). Similarly, increases in species richness may be the result of colonization by common species (Case 1996; Lennon et al. 2004; but see Gaston [2010] for an alternative view). However, many rare species are only common in areas where land use is traditional (e.g., where there have been centuries of extensive grazing and mowing), and such areas are maintained by land use of moderate intensity rather than high stocking rates and artificial fertilizers (Baur et al. 2006; Jackson et al. 2007). Likewise, there are clear limitations to using species richness as a basis for setting conservation priorities.

There are also caveats to our economic output model. For this model, we assumed that as intensity and extent of land use increase, economic output always increases proportionally. Payment-for-ecosystem-services schemes—such as Reducing Emission from Deforestation and Forest Degradation (REDD)—could fundamentally change the relation between economic returns and land-use intensity. Such payments may increase the amount of land with little or no land use by allowing land owners to receive economic benefits (i.e., direct payments) for conserving land. (Ghazoul et al. 2010). A full treatment of the effect of payments for ecosystem services on the results of our model was beyond the scope of this study though. Another practical extension of the model would be to relax the assumption of proportional increases in economic output due to land-use extent and intensity. This functional relation is likely heterogeneous in nonhomogenous landscapes, and extending the model to account for such changes in the model parameters is a necessary step in fitting our theoretical model to real-world landscapes.

Our results show that identifying the optimal relation between species richness and economic output requires knowing the functional relation between land-use intensity and species richness and understanding interactions between land use outside protected areas and species richness inside protected areas. Much past research on the effects of intensity of land use on species richness focused on the direction of change, rather than the functional form of the response of species richness to intensity of land use (McDonnell & Hahs 2008). When these functions are known, fine-resolution relations between land use alternatives can be estimated (Polasky et al. 2005; Nelson et al. 2008; Gagne & Fahrig 2010). Ecological research that explains changes in species richness in a format that is readily coupled with models of economic output is essential to moving beyond land-use debates and toward management plans.

Our results bring to focus 2 distinct areas in which land management can be improved. First, in our models, managing land-use intensity outside protected areas was key to conserving species richness (Hansen & DeFries 2007; Wade et al. 2011). We think managing land-use intensity outside protected areas is a major challenge because it is unlikely that many protected-area managers have training, time, or resources to focus on land-use planning beyond protected areas. Therefore, we stress that protected areas cannot be thought of as separate from the larger landscape and that, indeed, the success of protected areas is partially dependent on the landscape that surrounds them.

Second, the nonlinear relation between species richness and economic output highlights the possible dramatic results of attempting optimization, but failing. Land-use change is generally considered irreversible, at least in the short term; thus, unexpected changes can have long-term ecological effects. In our models, optimization of economic output was often associated with large changes in species richness, and incorrect assumptions about land use or species response could result in substantial decreases in species richness. We interpret this result as a call to adopt cautious planning and adaptive management rather than search for optimal solutions.

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Supporting Information

A proof of the analytical solutions to the maximization problem is available online (Appendix S1). The authors are solely responsible for the content and functionality of this material. Queries (other than absence of the material) should be directed to the corresponding author.

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