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Spatial distribution of species populations, relative economic values, and the optimal size and number of reserves

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Abstract We examine the tradeoff between the number and average size of nature reserves. When the costs of enforcing reserve boundaries are negligible, we find analytically that the relative price of biodiversity has a positive impact on the optimal total reserved area but an ambiguous impact on the optimal number of reserves. Simulation modeling of floral diversity in a tropical timber concession reveals that the resolution of this ambiguity depends on spatial distributions of the populations of tree species: whether or not they are spatially aggregated (clumped). The impact of biodiversity price on optimal reserve number remains analytically ambiguous when enforcement costs are not negligible. Multiple reserves being economically superior to a single reserve now requires, in addition to aggregation, a biodiversity price that is sufficiently high to offset the effects of enforcement costs. Most of our simulation scenarios generate threshold biodiversity prices that do not exceed a leading estimate of the marginal value of a higher plant species in the bioprospecting literature. Several smaller reserves evidently can be economically superior to a single larger one even in the presence of enforcement costs.

Keywords Biodiversity · Conservation · Nature reserve · Spatial aggregation · Rainforest

JEL codes Q57 · Q23 · C15

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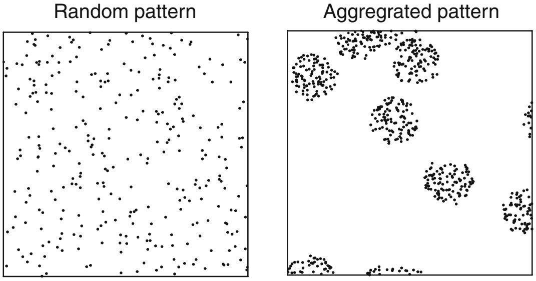

Fig. 1 Two extremes for the spatial patterning of conspecific individuals (trees of the same species)

1 Introduction

The design of nature reserve systems for conserving biological diversity has received substantial attention from economists during the past decade[1] and conservation biologists for much longer (Kingsland 2002). One of the most fundamental issues that has been debated is the tradeoff between the number of reserves and the size of reserves, which in the literature is known as the SLOSS ("single large or several small") debate. In this paper, we place this issue in an economic context by taking into account the benefits of reserves and their opportunity and administrative costs. We find that the optimal number of reserves cannot, in general, be determined independently of the optimal total area of the reserve system. The optimal number of reserves is scale-dependent, with the optimal scale of protection (total reserved area) depending on interactions between economic and ecological factors.

Among ecological factors, we highlight the importance of the spatial characteristics of natural communities, specifically the degree to which individuals of the same species (conspecific individuals) are aggregated. Aggregation refers to the tendency of individuals to be clumped instead of randomly located in the landscape. Figure 1 illustrates the difference between random placement and aggregation. Conspecific individuals are equally likely to be found anywhere in the landscape when they are randomly placed but not when they are aggregated. Aggregation tends to cause a subunit of a landscape, such as a reserve, to include fewer species, especially when the subunit is small (Coleman 1981; Plotkin et al. 2000a,b; He and Legendre 2002). Conversely, it tends to increase the populations of the species a subunit does contain, which increases the viability of the protected populations. It thus can be expected to influence the effects of both reserve number and reserve size on the long-run number of species conserved in a reserve system.

Aggregation has not been incorporated into previous economic reserve design models. It was implicit in arguments made by conservation biologists in the 1970s and 1980s. For example, Diamond (1976, p. 1028), a strong proponent of single large reserves, acknowledged that "each small refuge might save a different member of a set of mutually exclusive competitors."[2] We make the role of aggregation more explicit and use a combination of analytical and simulation methods to draw out its relevance for economic decisions. We also demonstrate that, as suggested above, its impact is influenced by species' minimum viable populations. To do this, we simulate not just

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[1] See Ando et al. (1998), Polasky and Solow (1999), and Polasky et al. (2001a).

[2] Laurance et al. (2002) (p. 607) similarly referred to a "sample effect," commenting that "Pronounced clumping means that many species will be missing from any particular fragment or reserve simply because they never occurred there in the first place."

the presence or absence of species within reserves, as in most economic studies (e.g., Ando et al. 1998; Polasky et al. 2000, 2001a), but also their abundances: the number of individuals of each species in a reserve. Polasky et al. (2001a, p. 76), among others, have observed that abundance is an important consideration in making conservation decisions but creates challenges for both modeling and data collection. In perhaps the most spatially detailed economic reserve study to date, Nalle et al. (2004) modeled the empirical distributions of populations of two vertebrate species in Oregon, owls and porcupines.[3] We sacrifice the spatial detail that is possible when studying a particular empirical situation by instead using a simulation approach, which allows us to vary the degree of aggregation and observe its consequences for reserve decisions.

We focus on reserve decisions to conserve floral diversity in tropical rainforests. Recent analyses of spatial patterns in tropical forests have discovered that the overwhelming majority of tree species are aggregated (He et al. 1997; Condit et al. 2000; Plotkin et al. 2000a). The setting for our simulation model is a tropical timber concession, in which the social objective is to maximize the sum of net benefits from timber production and biodiversity conservation. This framing of the problem enables us to connect the analysis to policy issues raised by international certification systems for sustainable forest management, which require the retention of unlogged areas within concessions.

Most of the previous reserve literature (e.g., Terborgh 1975; Diamond 1976), including nearly all economic studies (e.g., Montgomery et al. 1994, 1999; Polasky et al. 2001a,b; Lichtenstein and Montgomery 2003; Nalle et al. 2004), has focused on faunal diversity instead of floral diversity. Exceptions include studies by Ando et al. (1998), who included endangered species of both plants and animals in their study of reserve selection across the entire U.S., and Juutinen et al. (2004), who included 103 species of vascular plants among the more than 600 species that they considered in their study of reserve selection in Finnish forests.[4] Neither of these studies commented on the effects of aggregation of species populations on reserve decisions. We will cite evidence that many animal populations are aggregated, which suggests that qualitative aspects of our findings are relevant to the conservation of faunal diversity.

Our study also differs from many previous economic ones by examining multiple species instead of just one or two (Hyde 1989; Montgomery et al. 1994; Hof and Raphael 1997; Rohweder et al. 2000; Calkin et al. 2002; Nalle et al. 2004). Previous economic studies that have examined large numbers of species include the ones by Ando et al. (1998) and Juutinen et al. (2004) and also ones by Polasky et al. (2000, 2001a). Our study differs from theirs in not being a reserve site selection study in the literal sense, by which we mean a study that starts with a known set of sites that can potentially be reserved and then uses integer programming to select the subset that maximizes the number of species protected subject to a given site or budget constraint. Instead, we start with an undisturbed landscape and endogenously define sites by selecting total reserved area, number of reserves, and hence average reserve size. Ours is thus more accurately described as a reserve design study.

The paper is organized as follows. We begin by reviewing information on spatial patterning of tropical tree species from recent ecological studies. We then present an

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[3] Juutinen et al. (2004) included crude measures of abundance in their study but did not relate them to minimum viable levels.

[4] Haight et al. (2000) examined the selection of reserves to conserve vegetation communities but not individual plant species.

analytical model of the optimal choice of total reserved area and number of reserves. This model identifies ambiguities that motivate our simulation modeling. Next, we present the mathematical formulation of our simulation model, and we explain how we chose the values of key parameters in it. We then present our simulation results. We conclude the paper by summarizing our findings and the contributions they make to the reserve design literature.

2 Aggregation

Spatial aggregation of tree species in closed-canopy tropical forests results from limited seed dispersal ("the apple doesn't fall far from the tree") and habitat specialization (e.g., some species colonize only gaps). Evidence on aggregation in tropical forests comes mainly from permanent sample plots established during the past two decades by the Smithsonian Tropical Research Institute's Center for Tropical Forest Science.[5] For example, He et al. (1997) reported that 80 percent of the 814 tree species in a 50-hectare rainforest plot in Peninsular Malaysia had spatial distributions better described as aggregated than random. Although 50 hectares is small from a landscape perspective, it is large by the standards of botanical research. This may explain why earlier studies did not draw attention to the high degree of aggregation of tropical trees.

Little information exists on aggregation at scales above 50 hectares. Are the clumps themselves aggregated, as a model of self-similarity in ecosystem structure would suggest, or do they tend toward a more random distribution? A study by Plotkin and Muller-Landau (2002) suggests the latter: aggregation decreases with scale. Like the study by He et al. (1997), however, their study is based on data from a 50-hectare plot (in Panama). Studies on aggregation have yet to be conducted at scales measured in square kilometers instead of hectares.

Although our focus is on the aggregation of tree species, our results have bearing on the design of faunal reserves. Many animals, especially invertebrates, are associated with particular tree species through pollination or herbivory. If trees are aggregated, then such animals are likely to be, too. A frequently cited study of nearly 90 animal species by Taylor et al. (1978) found that only one species had populations that were randomly distributed at all densities. The study examined mainly insects and other arthropods, but it also included a selection of nearly two dozen protozoans, annelids, mollusks, echinoderms, fish, birds, and mammals. Of course, differences between plants and animals in terms of mobility and minimum viable populations imply that a reserve system that is designed to be optimal for floral conservation is unlikely to be optimal for faunal conservation too. In both cases, however, aggregation should have similar qualitative impacts on such features as the relative superiority of a few or many reserves.

3 Analytical model of an optimal reserve system

The analytical model in this section yields two propositions that motivate our simulation modeling. First, when the costs of administering the reserve system are negligible,

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[5] See www.ctfs.si.edu/sites/sites.htm for information on these plots.

an increase in the unit value of biodiversity increases the optimal total reserved area but has an ambiguous impact on the optimal number of reserves. Second, when administrative costs are not negligible and the total area of the reserve system is given, an increase in administrative costs decreases the optimal number of reserves while an increase in unit biodiversity value again has an ambiguous impact. Our simulation results reveal that the degree of aggregation has a crucial impact on the resolution of these ambiguities related to optimal reserve number.

Our analysis draws on results in a mathematical economics paper by Sah and Zhao (1998). In Extension 3 at the end of their paper, they examined the maximization of a function $f(x, n; \theta)$, where x is a continuous choice variable, n is a choice variable that has integer values, and θ is a continuous parameter. They showed that if f is strictly concave in x and n and differentiable in θ, and if the optimal solution $(x(\theta), n(\theta))$ is interior, then the continuous variable has a unique optimal value while the integer variable can have at most two optimal values. They also identified an additional condition that must be satisfied for the envelope theorem to hold. The envelope theorem ensures that the extreme value function $e(\theta)$, which gives the maximal value of f for a given value of θ (e.g., it is a profit function), can be differentiated with respect to θ, with $e_\theta(\theta) = f_\theta(x, n; \theta)$. The additional condition is that the integer variable has either a unique optimal value or, if it has two, that the derivative $f_\theta(x, n; \theta)$ is the same at both values.

3.1 Model structure and assumptions

Like most authors of previous studies on biodiversity conservation in forests (e.g. Juutinen et al. 2004), we assume that biodiversity is conserved only within the reserve system. We ignore the possibility that production systems, such as managed forests, might contain significant amounts of biodiversity (Boscolo and Vincent 2003; Lichtenstein and Montgomery 2003) and might interact with reserves spatially, dynamically, or both (Nalle et al. 2004). Reserves in our model are best viewed as isolated islands of undisturbed nature in a landscape where human action has otherwise essentially eliminated biodiversity.

Let A be the area of a contiguous block of forestland within which reserves are to be established. a is the total reserved area ($0 \leq a \leq A$), and m is the number of reserves. Average reserve size is thus a/m. The total amount of biodiversity in the reserve system is a function of both total reserved area and number of reserves: $S[a, m]$. (We use square brackets to indicate the arguments in a function and parentheses to indicate mathematical operations.) This is the production function for biodiversity. The most straightforward interpretation of S is the number of species in the reserve system, but at the level of abstraction in our analytical model it can be thought of as an index that also reflects other dimensions of biodiversity, such as endemism and genetic relatedness (Margules et al. 1982; Polasky et al. 2001b). We make no assumptions about S other than that it is strictly concave in a and m and continuously differentiable in a, with $S_a > 0$: in keeping with ecological theory, more biodiversity is conserved if the total reserved area is larger.

Concavity might seem like a strong assumption in view of theoretical and empirical evidence that forestry production sets can be nonconvex (Swallow et al. 1990; Boscolo and Vincent 2003). But in fact, this assumption serves to highlight the effects of our nonlinearity of interest, spatial aggregation, by ensuring that we are not inadvertently attributing those effects to nonconvexities. If S were continuously differentiable in m

in addition to a, then the conditions for strict concavity would be $S_{aa} < 0, S_{mm} < 0$, and $S_{aa}S_{mm} - S_{am}^2 > 0$. Generalizing from Sah and Zhao (1998, p. 628), the corresponding conditions when m is an integer are

$$S_{aa} < 0$$
$$\frac{\Delta^2 S}{\Delta m^2} < 0$$
$$S_{aa}\frac{\Delta^2 S}{\Delta m^2} - \left(\frac{\Delta S_a}{\Delta m}\right)^2 > 0,$$

where $\frac{\Delta^2 S}{\Delta m^2} \equiv \left(S\left[a,m+1\right] - S\left[a,m\right]\right) - \left(S\left[a,m\right] - S\left[a,m-1\right]\right)$ and $\frac{\Delta S_a}{\Delta m} \equiv S_a\left[a,m+1\right] - S_a\left[a,m\right]$.[6]

The economic benefits furnished by the reserve system are a linear function of biodiversity, pS, where p is the value (price) of a unit of biodiversity. In practice, the marginal value of biodiversity could diminish.[7] We assume a linear value function to highlight the economic implications of the ecological characteristics of S. Land outside the reserve system is valued for timber production, with a constant per-hectare value of timberland. Most economic studies of reserve site selection have emphasized the need to account for differences in opportunity costs across sites in making cost-effective conservation decisions.[8] This is a valid and important point, but there is no need for us to reaffirm it through our modeling.[9] The per-hectare value of timberland is the numeraire in our model, and so total timberland value is simply $A - a$.

3.2 Propositions

We consider the optimal selection of a and m under two scenarios: administrative costs of the reserve system are negligible, or not. Within administrative costs, we focus on the costs of monitoring and enforcing reserve boundaries. The world's most biodiversity-rich terrestrial ecosystems are found in tropical developing countries. Protected areas in these countries are at a high risk of encroachment by smallholders and commercial logging. Programs to demarcate and guard the boundaries of protected areas have been found to reduce these risks, despite institutional weaknesses in the countries (Bruner et al. 2001).

When enforcement costs are negligible, the economic objective is to maximize

$$W\left[a,m\right] = pS\left[a,m\right] + \left(A - a\right). \tag{1}$$

The profit function for this objective is $\pi\left[p\right] \equiv pS\left[a\left[p\right], m\left[p\right]\right] + \left(A - a\left[p\right]\right)$.

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[6] This definition of $\Delta S_a/\Delta m$ is based on the right-hand change in m. Using the left-hand change, it would be $S_a\left[a,m\right] - S_a\left[a,m-1\right]$.

[7] For example, bioprospecting values might diminish as more species are protected due to the redundancy of "leads" for new pharmaceuticals (Simpson et al. 1996).

[8] The opportunity cost of protection could be endogenous in addition to varying across sites. For example, an increase in total reserved area could raise timber prices due to a reduction in timber supply or a loss of scale economies in logging.

[9] Another interpretation is that variation in timberland values is negligible at the scale we are considering. Although our analytical model does not have a specified scale, our simulation model refers to a 100 km^2 timber concession. The terrain within concessions of this size is typically relatively uniform (e.g., all upland or all lowland), and so is distance to market. In addition, in Southeast Asia the numerous timber species are aggregated into a much smaller set of groups with uniform prices.

Proposition 1 *When enforcement costs are negligible and biodiversity is a strictly concave function of total reserved area and number of reserves, an increase in the price of biodiversity increases the optimal total reserved area but has an ambiguous impact on the optimal number of reserves.*

Proof W is strictly concave under the assumption that S is strictly concave. Assuming an interior solution ($a^*[p] \neq 0$), which is the only interesting case for this proposition, $a^*[p]$ is unique and $m^*[p]$ has at most two values (Sah and Zhao 1998). Assuming in addition that $m^*[p]$ is unique, which is consistent with the simulation results we present later, the envelope theorem holds and $\pi_p = S[a,m]$ (Sah and Zhao 1998). If S were continuously differentiable in both a and m, then duality between the production and profit functions would imply that $\frac{da^*}{dp} = \frac{-S_{mm}}{S_{aa}S_{mm}-S_{am}^2}$ and $\frac{dm^*}{dp} = \frac{S_{am}}{S_{aa}S_{mm}-S_{am}^2}$ (Chambers 1988, p. 144). With m an integer, the corresponding expressions are $\frac{da^*}{dp} = \frac{-\frac{\Delta^2 S}{\Delta m^2}}{S_{aa}\frac{\Delta^2 S}{\Delta m^2}-\left(\frac{\Delta S_a}{\Delta m}\right)^2}$ and $\frac{\Delta m^*}{\Delta p} \cong \frac{\frac{\Delta S_a}{\Delta m}}{S_{aa}\frac{\Delta^2 S}{\Delta m^2}-\left(\frac{\Delta S_a}{\Delta m}\right)^2}$. The first expression is positive due to the strict concavity of S, but the second expression cannot be signed because our assumptions about S place no restrictions on the sign of $\Delta S_a/\Delta m$. □

The ambiguity of $\Delta S_a/\Delta m$ can be stated as follows: does the marginal (and positive) impact of reserve area on biodiversity rise or fall as the number of reserves rises? Our simulation results will show that the answer depends on the degree of aggregation of species' populations and its interaction with minimum viable population size.

When enforcement costs are not negligible and are proportional to the total length of reserve boundaries, the objective is to maximize

$$\widetilde{W}[a,m] = pS[a,m] + (A-a) - wL[a,m], \qquad (2)$$

where w is the unit cost of enforcement and $L[a,m]$ is the total length of reserve boundaries. We assume that boundary length is increasing in both total reserved area and number of reserves: $L_a > 0$ and $\Delta L/\Delta m > 0$. These are reasonable assumptions. For example, if reserves are equal in shape and size, then basic geometry implies that boundary length increases if the reserve system either is larger or contains more reserves. We note that the term $-wL[a,m]$ is probably not concave. For example, if reserves are equal-sized and are square or circular, then it is proportional to $-w(am)^{1/2}$, which is strictly quasiconvex (Chiang 1984, p. 390 and Example 5 on p. 396). Nonconcavity of $-wL[a,m]$ creates the possibility that more than one pair of values of a and m could maximize $\widetilde{W}$. Despite this, we will assume that $\widetilde{W}$ is strictly concave, with a unique interior solution, which is consistent with our simulation results.

The following proposition holds for the maximization of $\widetilde{W}$, conditional on total reserved area being fixed at $a = \bar{a}$ (i.e., only the number of reserves is being chosen).

Proposition 2 *When enforcement costs are proportional to the total length of reserve boundaries and the net value function for land use is strictly concave, and when total reserved area is given, an increase in unit enforcement cost decreases the optimal number of reserves while an increase in the price of biodiversity has an ambiguous impact on the optimal number.*

Proof Parallel to the proof of Proposition 1. We obtain $\left.\frac{\Delta m^*}{\Delta w}\right|_{a=\bar{a}} \cong \frac{\frac{\Delta L}{\Delta m}}{p\frac{\Delta^2 S}{\Delta m^2}-w\frac{\Delta^2 L}{\Delta m}}$ and $\left.\frac{\Delta m^*}{\Delta p}\right|_{a=\bar{a}} \cong \frac{-\frac{\Delta S}{\Delta m}}{p\frac{\Delta^2 S}{\Delta m^2}-w\frac{\Delta^2 L}{\Delta m}}$. The first expression is negative due to the strict concavity of

$\widetilde{W}$ and the positive impact of m on L, but the second expression cannot be signed because our assumptions about S place no restrictions on the sign of $\Delta S/\Delta m$. □

The negative sign on $\Delta m^*/\Delta w|_{a=\bar{a}}$ is consistent with intuition, that an increase in enforcement costs should favor a system with a lower ratio of boundary length to area and thus reduce the optimal number of reserves (Simberloff and Abele 1976; Soulé and Simberloff 1986). We will see in the simulation analysis that aggregation tends to make $\Delta m^*/\Delta p|_{a=\bar{a}}$ positive and that a higher minimum viable population raises the threshold biodiversity price that switches the optimal number of reserves from one to two. These effects reflect the impacts of aggregation and minimum viable population on $\Delta S/\Delta m$.

4 Simulation model

As just demonstrated, the effects of prices on optimal reserve number can be theoretically ambiguous even under assumptions that might be regarded as restrictive, such as strict concavity. We constructed a simulation model of a tropical rainforest to study how aggregation influences price effects. The model is based on sampling theory. It predicts the expected number of species in a reserve system that has a given total area, a given number of reserves, a given degree of aggregation of the species it contains, and a given minimum viable population. It is analogous to an urn containing balls of different colors. The urn represents the forest, a ball represents an individual tree, and color indicates species. The number of balls is not the same for all colors, reflecting the fact that abundance varies across species. Samples from the urn represent reserves, and the number of samples represents the number of reserves. Aggregation corresponds to draws within a sample not being independent:[10] drawing a ball of a particular color raises the probability that other balls in the same sample have the same color. In contrast, random placement corresponds to independent draws, which result in a larger expected number of colors per sample. The total number of colors drawn (species protected) across a set of samples (reserves) thus depends on not only the number of samples (reserves) and number of draws per sample (average reserve size) but also on whether or not draws within a sample are independent (conspecific individuals are randomly placed or aggregated).

As this analogy indicates, the model is spatially *implicit*. It captures the statistical effects of aggregation without explicitly modeling the locations of individual trees. This approach enables us to investigate the effects of aggregation at a policy-relevant scale of thousands of hectares despite the lack of spatially explicit data on tropical rainforests for areas above 50 hectares. It also vastly simplifies computational issues, which Polasky et al. (2000, p. 2) note escalate rapidly in spatially explicit integer-programming models of reserve site selection as the numbers of potential and selected reserves increase. On the other hand, a limitation of the model compared to say, the Nalle et al. (2004) model of wildlife conservation in Oregon, is that it does not provide information on other spatial features of the simulated reserve system. For example, it does not indicate which reserves contain which species, nor does it indicate the locations of reserves relative to each other.

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[10] But draws between samples are independent. Indeed, independence between draws is what distinguishes one sample from another.

Several simplifications should be noted. First, we take the degree of aggregation of conspecific trees as given. We do not attempt to explain the processes that underlie spatial diversity patterns, which is an active area of ecological research (Plotkin et al. 2002). Second, we assume that the degree of aggregation is the same for all species. We comment on the empirical validity of this assumption below. Third, as a consequence of the particular statistical distribution that underlies our simulation model—the negative binomial distribution—we constrain reserves within a given reserve system to have the same size. We suspect, but do not prove, that the assumption of a common degree of aggregation across species implies that equal-sized reserves are optimal. This is an area for future research. Finally, we ignore potential increases in the number of species within reserves over time due to immigration and speciation. The number of species changes only if a reserve contains less than the minimum viable population of one or more species. We assume the same minimum viable population for all species, but we bracket this parameter using estimates reported in the literature.

4.1 Mathematical structure

A, a, and m are defined as in the analytical model: total area of forest, total reserved area, and number of reserves. As just noted, all reserves have the same area, a/m. S is now simply the total number of species in the reserve system. We ignore other aspects of biodiversity, including endemism and genetic relatedness. This simplified approach to quantifying biodiversity is typical of empirical and simulation studies that involve multiple species (e.g., Ando et al. 1998; Polasky et al. 2001a; Juutinen et al. 2004).

The original, undisturbed forest contains N individual trees of $\hat{S}$ different species. N_i is the number of trees of species i; $\sum_i N_i = N$. We make the standard theoretical assumption that stem density—the number of trees per unit area summed across all species—is constant throughout the forest (May 1975). This assumption is generally empirically valid for closed-canopy forests (Hubbell 2001), including tropical forests (Plotkin and Muller-Landau 2002). The value of the stem density parameter is thus given by $d = N/A$, and the number of trees in a reserve of area a/m is given by $n = da/m$.

We follow previous authors in using the negative binomial distribution to model spatial aggregation of conspecific trees (Wright 1991; He and Gaston 2000; He and Legendre 2002; Plotkin and Muller-Landau 2002). If n_i denotes the number of individuals of species i in a reserve containing n trees and $\hat{n}$ denotes the minimum viable population of a species within a reserve, then the probability that n_i is less than $\hat{n}$ is given by

$$P_{NBD}\left\{n_i < \hat{n}\right\} = \sum_{j=0}^{\hat{n}-1} \frac{(j+k-1)!}{j!(k-1)!}\left[\frac{k}{k+\bar{n}_i}\right]^k \cdot \left[\frac{\bar{n}_i}{k+\bar{n}_i}\right]^j. \tag{3}$$

$\bar{n}_i$ is the expected number of individuals of species i in a reserve containing n trees, ignoring spatial patterning. It is calculated as $n\frac{N_i}{N}$. k is the clumping parameter. Spatial patterns become more random as k tends toward positive infinity and more aggregated as it tends toward zero. Both k and $\hat{n}$ are assumed to be the same across species.

Given data on species abundances (the N_is), the density parameter (d), and the clumping parameter (k), one can use the following expression to calculate the probability that at least one of m reserves contains $\hat{n}$ individuals (a viable population) of species i:

$$P_{NBD}\left\{n_i \geq \hat{n}\right\} = 1 - \left(P_{NBD}\left\{n_i < \hat{n}\right\}\right)^m. \tag{4}$$

This expression implicitly defines reserves as noncontiguous spatial units. With $k \neq +\infty$, the probability $P_{NBD}\left\{n_i \geq \hat{n}\right\}$ is not the same for, say, 10 reserves of 100 hectares each as for 1 reserve of 1,000 hectares, even if $\hat{n} = 1$. The expected number of species that will survive in the set of m reserves is thus given by the sum,[11]

$$S_{NBD} = \sum_{i=1}^{S} P_{NBD}\left\{n_i \geq \hat{n}\right\}. \tag{5}$$

We calculated P_{NBD} using code drawn from the GNU Scientific Library (Gough 2003).

We are not the first in the reserve literature to use a probabilistic model. Our motivation differs from that behind the seminal applications by Haight et al. (2000) and Polasky et al. (2000), however. The motivation in those studies was to understand the impact of uncertainty about species presence on reserve site selection. Our motivation is to understand the impact of species' spatial distributions on reserve design. Although these distributions are poorly understood in tropical forests, our focus is not on this uncertainty per se. We use a probabilistic model because, through the choice of k, it enables us to vary the degree of aggregation and to examine the resulting impact on the number of species protected. We regard each realization of the simulation model as a plausible real-world realization under the ecological assumptions made, and we seek to identify central tendencies across the realizations. A comparison of means across scenarios, as opposed to an analysis of the effects of variation within a scenario, is thus our motivation.[12]

A limitation of the formulation of the negative binomial model in (3) is that it assumes sampling with replacement, which obviously does not correspond to the selection of spatially distinct, nonoverlapping reserves. The difference between sampling with and without replacement is negligible, however, when sample size is much smaller than population size (Johnson and Kotz 1969; Plotkin and Muller-Landau 2002). For this reason, we limit our analysis to cases where no more than 25 percent of the forest is protected ($a/A \leq 0.25$).

4.2 Area simulated and reserve number

The total area of forest (A) was assumed to be 10,000 hectares (= 100 km^2). This is an estimate of the minimum size of a sustained-yield timber concession in Southeast Asia. We arrived at this estimate by multiplying the timber cutting cycle under the Peninsular Malaysia Forestry Department's "Selective Management System," 30 years, by the planned annual cutting area in a timber concession in northern Peninsular Malaysia

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[11] We assume that population increases for species that survive in a reserve offset population losses for species that do not survive, and thus stem density is maintained at d.

[12] Because we are focusing on mean values, the optimal values we report do not correspond to the optimal values for each and every simulation realization. For this reason, the total reserved area and number of reserves that are optimal for a specific, actual forest area would likely differ from the values we report. The expected values across a set of areas should converge to values we report, however, as long as our distributional assumptions hold.

operated by Perak Integrated Timber Complex, approximately 300 hectares per year. This concession was the first in Peninsular Malaysia to be certified as sustainable by the Forest Stewardship Council (FSC). We simulated reserve numbers (m) from 1 to 30. The last number corresponds to a reserve being included in each annual cutting area within the concession.

Terborgh (1975) argued that individual reserves must cover thousands of square kilometers to have significant conservation value. This is an order of magnitude larger than our simulated forest. Our simulation analysis is nevertheless relevant to real-world conservation decisions, for two reasons. First, it is ecologically relevant due to our focus on floral diversity instead of faunal diversity, to which Terborgh's recommendation pertained. Although reserves within a 100 km^2 block of forestland might be too small to support viable populations of certain fauna, especially large predators, they might nevertheless be large enough to support populations of tree species for centuries.[13] Second, our analysis has relevance for certification systems for sustainable forest management. Although Soulé and Simberloff (1986) (p. 22) claimed that "The historical phase of establishing reserves is drawing to a close," leading timber certification systems require the inclusion of unlogged "refugia" within timber production forests.[14] To obtain FSC certification, Perak Integrated Timber Complex agreed to reserve slightly more than a quarter of its total concession area. Widespread implementation of such requirements could lead to a substantial increase in the number and area of reserves in tropical forests, as vastly more of those forests are currently classified for timber production than for nature protection.

4.3 Abundance, aggregation, and minimum viable population

We followed Condit et al. (2002) by including only trees with a stem diameter of at least 10 cm in our hypothetical forest. We set the density parameter (d) equal to 600 trees per hectare (Condit et al. 1996). Total community size (N) was thus 6,000,000 individual trees. We used Hubbell's unified neutral model (Hubbell 2001) to generate estimates of the total number of species ($\hat{S}$) and species abundances (N_i) in an undisturbed forest of this size.[15] We obtained an expected total number of species equal to 1,103, which is consistent with estimates for tropical rainforests (He et al.

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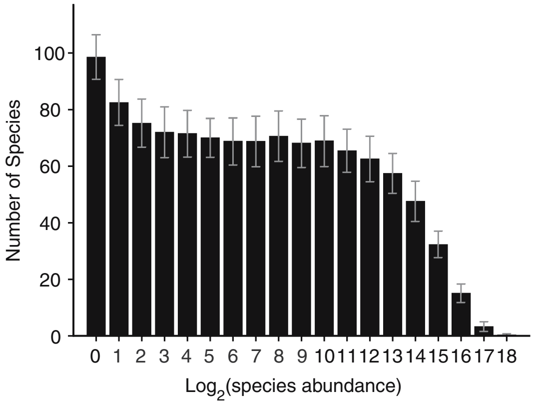
[13] Terborgh (1976) refers to profound changes in the composition of avian communities on land-bridge islands even though the vegetation changed little, and Soulé and Simberloff (1986) cite the persistence of plant species for thousands of years on sites of less than a square kilometer. Of course, if a particular tree species requires animals for pollination or dispersal, but a reserve is too small to support populations of those animals, then the tree species will eventually disappear from the reserve. Tree species have in fact been lost rapidly from small islands created by the Panama Canal (Leigh et al. 1993).

[14] For example, Indicator 5.7 of the International Tropical Timber Organization (1999) calls for the "Existence and implementation of management guidelines to ... keep undisturbed a part of each production forest ...." The Forest Stewardship Council (2002) has similar similar requirements (e.g., its Criteria 6.2 and 9.3). Moreover, forested landscapes on the order of hundreds of square kilometers have been regarded as "reasonable planning units" by studies in other parts of the world (e.g., Montgomery et al. 1999; Juutinen et al. 2004, p. 536).

[15] Hubbell's model includes a parameter θ, which has a value of approximately 100 in tropical forests (Condit et al. 1996). Given estimates of θ and N, it generates a species abundance distribution as follows. Individual trees are added to the simulated forest sequentially. The probability that the jth individual is a new species is equal to $\theta/(\theta + j + 1)$. If the jth individual is not a new species then it is one of the existing species with probability equal to the relative abundances of the existing species.

Fig. 2 Species abundance distribution derived from Hubbell's unified neutral theory, for an undisturbed forest of 6,000,000 individual trees. Estimates based on 100 realizations. Error bars show standard deviations. The expected total number of species is 1103



1997; Laurance et al. 2000). Figure 2 shows the abundance distribution generated by Hubbell's model.

Evidence summarized earlier indicates that tropical trees are highly aggregated at small scales, with the degree of aggregation being more poorly understood at larger scales but probably becoming weaker. Empirical studies at scales up to 50 hectares that have measured aggregation using the negative binomial model have found that the clumping parameter k varies across species, with a median value of about 0.1 (Condit et al. 2000; Plotkin and Muller-Landau 2002). These studies find that a power law best explains the scale dependence of k, at least over short distances.[16] In view of the narrow information base on the relationship between aggregation and spatial scale, we conducted the simulation analysis under two scenarios: first, the clumping parameter has the fixed value 0.1; and second, it increases with reserve size and is given by the power-law function $k = 0.1 + 0.0001(a/m)^{0.5}$ (Plotkin and Muller-Landau 2002).

We calculated the expected long-run number of species in the reserves under two assumptions about the minimum viable population, $\hat{n} = 100$ and $\hat{n} = 1000$. The former is an estimate of the actual populations of plant species when they are listed as threatened or endangered (Wilcove et al. 1993). The latter is, according to Thomas (1990) (p. 326), "adequate for species of normal [population] variability." These values bracket the oft-cited population size proposed by Franklin (1980) and Soulé (1980) as being sufficient for long-term maintenance of genetic variability, 500, which Dick et al. (2003) used recently to estimate the minimum area that must be reserved to protect the tropical tree species *Dinizia excelsa*.[17]

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[16] There is no evidence of a significant correlation between abundance and aggregation (Plotkin et al. 2000a), which could confound our simulation results.

[17] Our model ignores the possibility of gene flow between reserves through long-range pollen dispersal. Unlike temperate trees, tropical trees are overwhelmingly animal-pollinated, not wind-pollinated. With some exceptions (Dick et al. 2003), animal vectors tend to travel short distances in tropical rainforests (Nason et al. 1998).

4.4 Enforcement costs

From (2), when total reserved area is fixed at $\bar{a}$, two reserves are superior to a single one if and only if the following inequality holds:

$$pS\left[\bar{a},2\right]-wL\left[\bar{a},2\right]>pS\left[\bar{a},1\right]-wL\left[\bar{a},1\right]. \tag{6}$$

This can be reorganized to yield

$$p\frac{\Delta S}{\Delta m}>w\frac{\Delta L}{\Delta m}, \tag{7}$$

which relates to the numerators in the two expressions in the proof of Proposition 2. A shift from one reserve to two is justified if and only if it increases the amount of biodiversity conserved—$\Delta S/\Delta m$ is positive—and the value of that increase exceeds the increased enforcement cost stemming from the greater boundary length of the reserve system. We used (6) to calculate the threshold value of a species that induced this shift and (7) to interpret the results.

We needed an estimate of the unit cost of enforcement, w, to determine the threshold value of p from (6). We calculated a liberal estimate of w—one that we believe overstates the actual cost of enforcing reserve boundaries—to reduce the risk of understating the threshold value of p. We calculated it for Malaysia, which is the source of most of our ecological and forestry data. According to the World Conservation Monitoring Center's on-line database,[18] Malaysia had 54 protected areas covering 14,848 square kilometers in 1996. Nearly a third of the area, 4,343 square kilometers, was in the country's original national park, Taman Negara; the rest was in much smaller areas. We assumed that reserves are circular, which is the shape that minimizes boundary length for a given area (McDonnell et al. 2002). Under this assumption and an additional one that the 53 reserves other than Taman Negara are equal-sized,[19] the total boundary length of the system was 2,879 kilometers. Data in James et al. (1999) (pp. 6, 32) for a sample of protected areas in the country indicated that the 1994 budget per square kilometer was US$2,061 (1996 prices). This was the second highest amount for tropical developing countries in Southeast Asia. Multiplying this amount by the total area of the system, and dividing by our estimate of total boundary length, gave an estimate of US$10,631 per kilometer.

To arrive at our final estimate of w, we multiplied this amount by 1.71, which is the ratio of required funding to actual budgets in Southeast Asia according to James et al. (1999) (p. 14). Our final estimate was thus US$18,217 per kilometer. This is a liberal estimate for four reasons. The first two were mentioned in the previous paragraph: the assumption of circular reserves, and Malaysia's high (for Southeast Asia) budget per square kilometer of protected area. The third is that the budget data refer to all expenditures, not just expenditures directly related to patrolling boundaries. The fourth is that the Malaysian correspondent for the James et al. (1999) study did not report a budget shortfall, unlike the correspondents for many other Asian countries.

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[18] www. wcmc.org.uk/protected_areas/data/summstat.html.

[19] This is of course not strictly true, but it does not substantially bias our estimate of total length because Taman Negara accounts for so much of the total area.

5 Simulation results

We assumed in the analytical model that the biodiversity production function $S[a, m]$ is strictly concave, and we pointed out that this assumption is not sufficient for the objective function $W[a, m]$ to be strictly concave when it includes enforcement costs. We checked whether the counterparts of these functions in the simulation model have unique maxima by mapping out the solution surfaces for values of m ranging from 1 to 30 and values of a/A at 0.01 intervals up to 0.25. We found that the solution surfaces had single peaks within these ranges. We are therefore confident that solutions presented below are optimal within the range of values considered.

5.1 Enforcement costs are negligible

Figures 3–5 show the expected number of species with viable populations in the reserve system under different assumptions about aggregation, minimum viable population, total reserved area, and number of reserves. To reduce clutter, the figures show results for $m = 1, 2, 5, 10, 15$, and 30 instead of the full set of curves from 1 to 30.

Figure 3 shows results for the case of random placement, with results for $\hat{n} = 100$ in panel a and $\hat{n} = 1000$ in panel b. For a given total reserved area, the number of species is always larger when the number of reserves is smaller. This is true regardless of the total reserved area or the choice of $\hat{n}$, although the number of species is of course larger when $\hat{n}$ has the smaller value. For both values of $\hat{n}$, a single reserve always contains the maximum number of species.

Figure 4 shows the effects of introducing aggregation, with k constant at 0.1. Now, the number of species tends to be larger when the number of reserves is *larger*: the curves for $m = 10, 15$, and 30 (markers connected by solid lines) tend to be above the curves for $m = 1, 2$, and 5 (markers connected by dashed lines). The ranking is not constant, however. It depends on the total reserved area: it is scale-dependent. The advantage shifts toward a larger number of reserves as total reserved area rises. For $\hat{n} = 100$ (panel a) and the values of m shown, $m = 10$ contains the most species when $a/A \leq 0.05$, but $m = 15$ contains the most above this threshold. For $\hat{n} = 1000$ (panel b), $m = 2$ contains the most species when $a/A \leq 0.03$, $m = 5$ contains the most when $0.03 < a/A \leq 0.11$, and $m = 10$ contains the most for larger values of a/A. In combination, Figs. 3 and 4 show that aggregation and minimum viable population work in opposite directions in determining the optimal number of reserves. Aggregation tends to raise the number,[20] while minimum viable population tends to reduce it.

We found in the section on the analytical model that an increase in the price of biodiversity raises the optimal total reserved area but has an ambiguous impact on the optimal number of reserves. We can relate these findings to the results in Figs. 3 and 4 if, following Rohweder et al. (2000), Calkin et al. (2002), Boscolo and Vincent (2003), and Lichtenstein and Montgomery (2003), we interpret the outer envelope of

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[20] This contrasts with results in the literature on nonlinearities in multiple-use forestry production sets, which emphasizes that nonlinearities—in particular, nonconvexities—tend to favor specialized land use (Bowes and Krutilla 1989). For example, Boscolo and Vincent (2003) find that a nonconvexity due to fixed logging costs causes the spatial concentration of biodiversity conservation to be economically superior to a more spatially dispersed approach. In our model, spatially concentrated conservation corresponds to a single large reserve, while a spatially dispersed approach corresponds to several smaller ones. The relative superiority of these two approaches again turns on a nonlinearity, i.e. conspecific aggregation. But in contrast to fixed logging costs, this nonlinearity is an ecological one, and it has the opposite impact: it favors a more dispersed conservation approach.

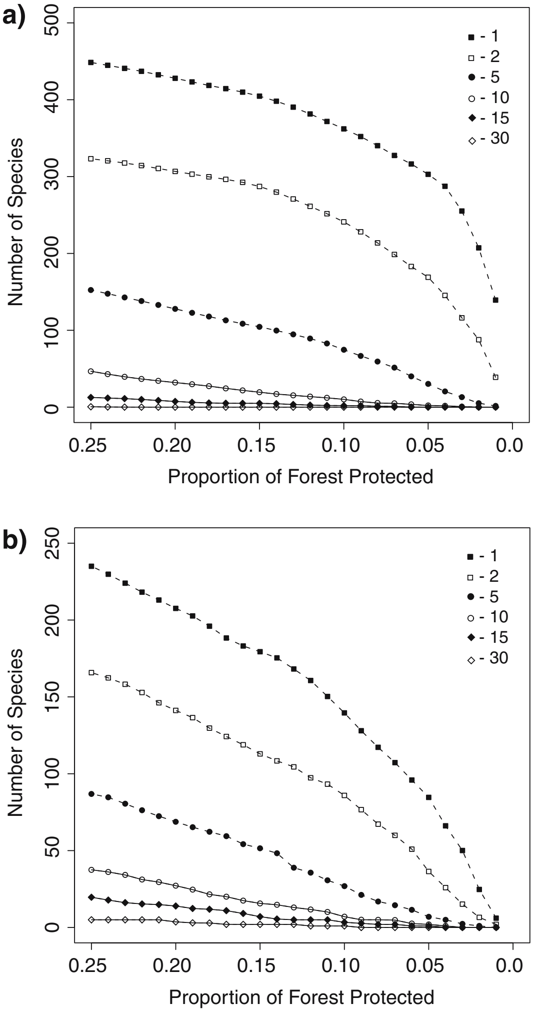

Fig. 3 Expected number of tree species summed across reserves: conspecific individuals are randomly placed. Number of reserves: ■ = 1; □ = 2; ● = 5; ○ = 10; ◆ = 15; ◇ = 30; markers for smaller (larger) number of reserves are connected by dashed (solid) lines. **Panel a**: minimum viable population $(\hat{n}) = 100$. **Panel b**: $\hat{n} = 1{,}000$

the curves for the different reserve numbers in the figures as the production possibilities frontier for the forest. The vertical axis shows production of biodiversity, while the horizontal axis shows timber harvest, which is proportional to the area that is *not* reserved. In both figures, the optimal production point moves leftward along the frontier as the price of biodiversity rises: protecting more of the forest makes economic sense, regardless of the presence or absence of aggregation; $\mathrm{d}a^*/\mathrm{d}p$ is unambiguously positive, as in Proposition 1.[21] In Fig. 4, the optimal number of reserves also rises as we move leftward along the frontier: $\Delta m^*/\Delta p > 0$. From the proof of Proposition 1, the necessary and sufficient condition for this result is $\Delta S_a/\Delta m > 0$. We can see that this condition holds in Fig. 4: for a given proportion of the forest reserved, the

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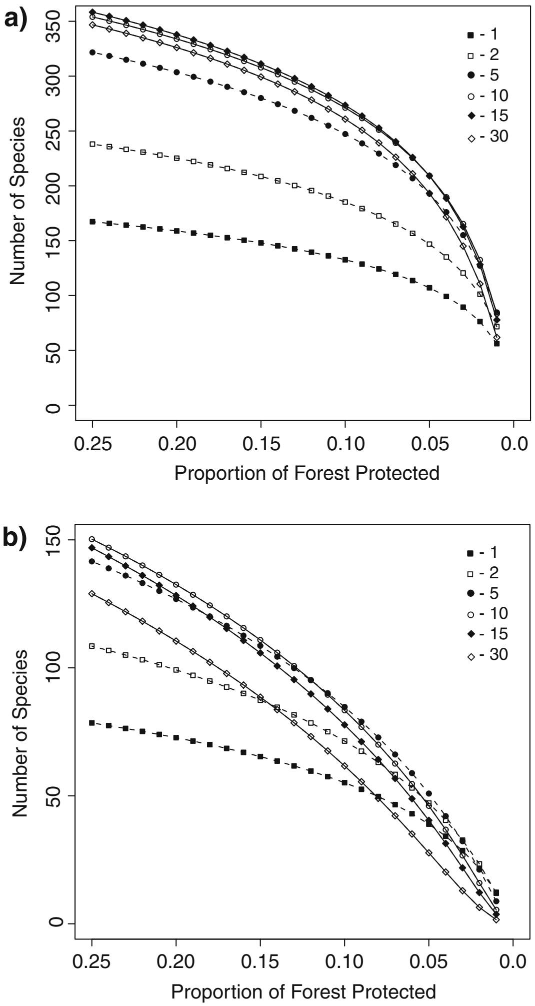
[21] The leftward flattening of the frontiers indicates that the marginal opportunity cost of conserving a species is rising. This is not a new finding, but previous studies have highlighted rising land acquisition costs as the explanation (e.g., Balmford et al. 2000). Our explanation is entirely ecological, as we assume a constant unit value of timberland.

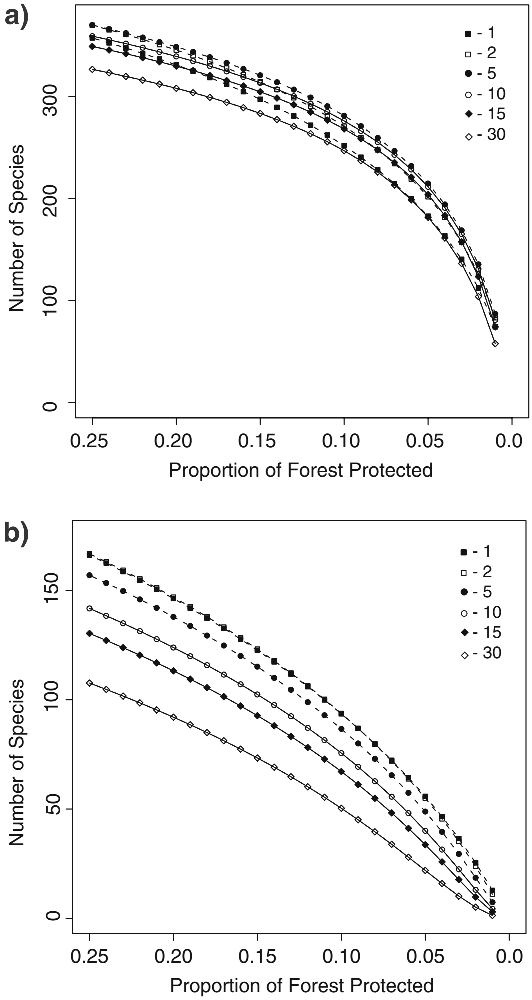
Fig. 4 Expected number of tree species summed across reserves: conspecific individuals are aggregated, and *k* is constant at 0.1. Symbols are same as in Fig. 3



slopes of the curves are steeper (S_a is larger) when the number of reserves is higher. In contrast, under random placement in Fig. 3, the slopes are less steep, which causes the curves grow farther apart—the absolute advantage of a single reserve over multiple reserve increases—as the proportion of protected forest rises.

Not surprisingly, Fig. 5 indicates that the results for *k* following a power law lie between those for random placement and aggregation with a constant *k*. The rankings are more similar to those in Fig. 3 when a larger area is protected, because individual reserves are then larger and spatial distributions are thus more random, but more similar to those in Fig. 4 when a smaller area is protected, because the reverse conditions hold. For $\hat{n} = 100$, $m = 5$ dominates over most of the range; for $\hat{n} = 1000$, $m = 1$ and $m = 2$ are about equally dominant. An increase in the price of biodiversity causes the optimal total reserved area to fall off about as rapidly as in Fig. 4 (the frontiers have similar position and curvature), but the reduction in the optimal number of reserves along the frontier is not nearly as pronounced.

Fig. 5 Expected number of tree species summed across reserves: conspecific individuals are aggregated, and *k* follows a power law (aggregation weakens with reserve size). Symbols are same as in Figs. 3 and 4



In no case, not even the strong aggregation case in Fig. 4, do we find support for including a reserve in each annual cutting area of the concession (i.e., $m = 30$). This implies that certification systems that require retention of unlogged refugia within tropical timber concessions have maximal impact on conservation of floral diversity only if they allow the agglomeration of refugia into larger reserves, though not necessarily just a single one.

5.2 Enforcement costs are not negligible

The results reported above indicate that multiple reserves are optimal only if species are aggregated. Enforcement costs reduce the net economic benefits of multiple reserves compared to a single reserve and thus, like minimum viable population, counter the effects of aggregation. Table 1 shows the threshold value of a species that is required to offset the US$18,217 per kilometer enforcement cost and change the

Table 1 Minimum value per species for two reserves to be economically superior to a single one when the enforcement cost is \$18,217 per kilometer

Proportion of forest protected (a/A)	Aggregation assumption	
	k is constant at 0.1	k follows power law
a. $\hat{n} = 100$		
0.05	\$1,654	\$3,393
0.10	\$1,762	\$4,802
0.15	\$1,868	\$6,757
0.20	\$1,964	\$9,459
0.25	\$2,051	\$13,336
b. $\hat{n} = 1000$		
0.05	\$7,381	*
0.10	\$5,694	\$77,653
0.15	\$5,277	\$73,266
0.20	\$5,124	\$97,732
0.25	\$5,068	\$179,523

* A single reserve contains the maximum number of species and so is optimal regardless of the value per species

optimal number of reserves from one to two.[22] The reserved proportion of the forest is indicated in the first column. The first thing to notice is that the threshold values are lower when aggregation is stronger: the values in the second column (constant k) are smaller than those in the third column (k follows power law) for both $\hat{n} = 100$ and $\hat{n} = 1000$. The explanation is straightforward. For a given total reserved area, increasing the number of reserves from one to two increases total boundary length and thus enforcement costs. Per expression (7), the increase in number of reserves is justified only if the benefits rise by an even greater amount. An increase in the number of reserves from one to two raises the number of species more when aggregation is stronger (Figs. 4 vs. 5), and so the value per species does not need to be as high to offset the increased enforcement costs in that case.

The second thing to notice is that the threshold values are much higher when the minimum viable population is higher ($\hat{n} = 1000$ vs. $\hat{n} = 100$). The explanation is again straightforward: an increase in the number of reserves from one to two does not raise the number of species as much when the minimum viable population is higher (panel b vs. panel a in either Figs. 4 or 5). In (7), $\Delta S/\Delta m$ is smaller. Hence, the value per species needs to be higher to justify such an increase.

Third, notice that the effect of an increase in the proportion of the forest protected on the threshold values depends on both the degree of aggregation and the minimum viable population. With total boundary length given by $L = 2\,(\pi am)^{1/2}$, an increase in a/A increases $\Delta L/\Delta m$, and from (7) this should tend to cause the threshold value to rise too if $\Delta S/\Delta m$ either falls or does not rise as rapidly. This is indeed the result for $\hat{n} = 100$: although $\Delta S/\Delta m$ rises with a/A when k is constant, it does not rise as rapidly as $\Delta L/\Delta m$, and it falls when k follows a power law. For $\hat{n} = 1000$ and k constant, however, $\Delta S/\Delta m$ rises so rapidly that the threshold value actually falls. For $\hat{n} = 1000$ and k following a power law, $\Delta S/\Delta m$ first rises and then falls, and so the threshold value follows the opposite pattern.

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[22] The threshold value must be even higher for more than two reserves to be optimal.

Finally, we point out that most of the values in the table are well below the marginal bioprospecting value of a higher plant species estimated by Simpson et al. (1996), US$9,431 as of the mid-1990s. This suggests that multiple reserves are indeed frequently optimal in tropical timber concessions. Two factors reinforce this conclusion. First, actual threshold values are probably even lower than the ones shown in Table 1, given our use of a liberal estimate of the unit cost of enforcement. Second, Rausser and Small (2000) argue that the genetic resource values of tropical forests are orders of magnitude larger than the estimate by Simpson et al.

6 Conclusions

We have examined the tradeoff between the number of reserves and their average size from an economic standpoint. We considered two cases that were defined by whether or not the costs of enforcing reserve boundaries are negligible. When these costs are negligible, we found analytically that an increase in the value of biodiversity relative to the opportunity cost of land has an unambiguously positive impact on the optimal total reserved area but an ambiguous impact on the optimal number of reserves. This ambiguity occurs even though we assume strict concavity of the biodiversity production function, and it stems from a feature of the biodiversity production function that is not restricted by this assumption. Through simulation modeling of floral diversity in a tropical timber concession, we found that spatial distributions of the populations of tree species affect resolution of this ambiguity. A single reserve is always optimal when individuals of a given species are randomly placed, meaning that they are equally likely to be found anywhere in the forest. Multiple reserves tend to be optimal when individuals are instead aggregated (clumped), which affects both the number of species and their populations in a unit area. In the presence of aggregation, an increase in the relative price of biodiversity increases not only the optimal total reserved area but also the optimal number of reserves. In this sense the optimal number of reserves depends on the scale of protection, which is determined by the relative price of biodiversity. The optimal number tends to be higher when aggregation is stronger or the minimum viable population is lower, but it is always less than 30, which is a typical number of annual harvest units in a sustained-yield tropical timber concession. Although the creation of reserves to conserve biodiversity in tropical timber concessions may make economic sense, the creation of a reserve in each annual harvest unit does not.

When enforcement costs are not negligible, we again found analytically that an increase in the relative price of biodiversity has an ambiguous impact on the optimal number of reserves. In contrast, the unit cost of enforcement has an unambiguously negative impact on the optimal number. Multiple reserves being economically superior to a single reserve now requires, in addition to aggregation, a biodiversity price that is sufficiently high to offset the effects of enforcement costs, which increase with reserve number. Most scenarios in our simulation modeling generated threshold biodiversity prices that do not exceed a leading estimate in the bioprospecting literature. This suggests that the creation of several smaller reserves in tropical timber concessions is indeed economically superior to the creation of a single large one. The threshold biodiversity prices are very sensitive to the degree of aggregation and to minimum viable popuation, and they can either rise or fall with the total area protected.

Our results underscore the fundamental importance of interactions between economic variables, such as prices, and ecological variables, such as aggregation and minimum viable population, for reserve decisions. Previous economic studies have also stressed this point (e.g., Ando et al. 1998; Polasky et al. 2001a). They have done so, however, largely in connection to decisions about the *selection* of reserves from a set with characteristics that are fixed and known (though not necessarily perfectly known; see Haight et al. (2000); Polasky et al. (2000)). We draw attention to the importance of economic and ecological interactions for the *design* of the characteristics of reserves. The literature on reserve design, as opposed to reserve selection, has long been dominated by ecological studies (Simberloff and Abele 1976; Soulé and Simberloff 1986). Our study indicates that economic analysis can shed light on important design issues. We consider just two aspects of reserve design—reserve number and, through its interaction with total reserved area, average reserve size—but they are arguably the most basic ones. The analytical and simulation methods that we have employed could perhaps be usefully deployed to examine other important design issues, such as reserve shape and connectivity between reserves.

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