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A probabilistic model of reserve design

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Abstract

We develop a probabilistic approach to optimum reserve design based on the species–area relationship. Specifically, we focus on the distribution of areas among a set of reserves maximizing biodiversity. We begin by presenting analytic solutions for the neutral case in which all species have the same colonization probability. The optimum size distribution is determined by the local-to-regional species richness ratio k. There is a critical k_t ratio defined by the number of reserves raised to the scaling exponent of the species–area relationship. Below k_t, a uniform area distribution across reserves maximizes biodiversity. Beyond k_t, biodiversity is maximized by allocating a certain area to one reserve and uniformly allocating the remaining area to the other reserves. We proceed by numerically exploring the robustness of our analytic results when departing from the neutral assumption of identical colonization probabilities across species.

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Keywords: Marine reserves; Island biogeography; Species–area; Power-laws; Nestedness; Colonization; Extinction

1. Introduction

The theory of island biogeography predicts the number of species in an island as a balance between colonization and extinction events (MacArthur and Wilson, 1967). The number of species s (hereafter biodiversity) of an island of area A can be described by the following power-law relationship:

$$s = cA^z, \tag{1}$$

where c is a fitted constant and the scaling exponent z has values in the range 0.2–0.4 (Williamson, 1988). Several explanations for the above species–area relationship have been proposed, including species abundance distributions (May, 1975), population dynamics (Hubbell, 2001), and the interplay between a skewed species abundance distribution and intraspecific spatial aggregation (García Martín and Goldenfeld, 2006). The small range of empirical z-values has recently been derived from the specific form of the

canonical lognormal species abundance distribution (Southwood et al., 2006), which served to unify the species–area relationship with two other power laws in ecology: species frequency versus species length, and maximal body size versus area (Southwood et al., 2006).

The theory of island biogeography has been used to generate simple rules of thumb in conservation biology. One classical example is the problem of choosing between one large or two small reserves. Higgs and Usher (1980) used the species–area relationship and elegantly showed that the answer depends on the species overlap, that is, the fraction of common species contained in both smaller reserves. Thus, it is better to have two reserves for low overlaps, whereas one reserve maximizes biodiversity if the overlap is larger than a specific threshold.

Here we extend the one versus two reserves approach (Higgs and Usher, 1980) for the case of multiple reserves. Given a set of r reserves, we ask the following questions: (i) what is the size distribution among these reserves that maximizes biodiversity? and (ii) how does this solution depend on the total protected area and regional diversity?

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Our analytic approximation assumes neutrality. MacArthur and Wilson (1967) assumed that all species are equivalent in the sense of having the same extinction and colonization rates (see also Hubbell, 2001 for an important generalization at the individual level). However, research in island biogeography since the decade of the 1980s has unequivocally shown that species are distributed non-randomly across reserves. Specifically, due to different colonization (and/or extinction) rates, some species are more widespread than others. The observed pattern is nested, in which species inhabiting small reserves form perfect subsets of the species inhabiting larger reserves (Darlington, 1957; Patterson, 1987; Atmar and Patterson, 1993; Cook and Quinn, 1998; Fischer and Lindenmayer, 2002). To assess to what extend these non-random patterns of species distribution affect our analytic results, we end up by analyzing numerically an extension of our model. We thus ask: (iii) how robust are our analytic results when non-neutral, species-specific colonization rates are incorporated? Our analytical approach differs from alternative approaches in reserve design such as site-selection algorithms (Nicholson et al., 2006; Cabeza and Moilanen, 2003; Arponen et al., 2005; Halpern et al., 2006; Wilson et al., 2006) that analyze real systems and predict the optimum set of reserves given some finite budget. Our paper presents an idealized system that, although necessarily simplistic, it is able to predict general, robust rules of thumb based on a few ubiquitous general laws such as the species–area relationship.

2. Maximizing biodiversity: two reserves

Let us start by illustrating the case of two reserves. Although this reproduces Higgs and Usher (1980), it will be important for our generalization to r reserves in the next section. Higgs and Usher (1980) assumed a fixed area distribution between both reserves and derived the critical species overlap dictating whether it is better to have a large reserve or two small ones. Our approach in here is slightly different: we assume that we have two reserves (r in the following section) and are able to tune the area distribution. That is, having in mind that the total area A satisfies $A = A_1 + A_2$, we can determine to our convenience p satisfying $A_1 = pA$ and $A_2 = (1 - p)A$. Let us assume that n is the regional number of species (i.e., the total number of species in the nearby continent). Each one of these species has a probability of colonizing any of the above reserves. The number of species s_1 in reserve 1 will be:

$$s_1 = cA_1^z = cA^z p^z, \tag{2}$$

and similarly, the second reserve will host s_2 species given by

$$s_2 = cA_2^z = cA^z (1 - p)^z. \tag{3}$$

The problem is then to calculate the value of p maximizing biodiversity, i.e., the total number of species in both reserves.

In a realistic scenario there are species with high colonization rates (these ones will likely appear in both reserves), and species with low colonization rates (we will hardly see any of these). Let us assume the following probability distribution of reserve colonization across the n species in the pool:

$$P(x) \propto x^{-\gamma}, \tag{4}$$

with $x = 1, 2, \ldots, n$.

Notice that the above probability distribution would produce a nested pattern as found in island biogeography (Darlington, 1957; Patterson, 1987; Atmar and Patterson, 1993). For example, only the species with the highest colonization probability would be found in the far distant reserve, while this and the other species would be found in the closest reserve. That is, species in remote reserves form well-defined subsets of the species found in close reserves.

To be able to derive analytical results, we start by assuming that every species has the same colonization rate. This corresponds to the limiting case $\gamma = 0$, that is, a uniform colonization probability distribution. This neutral scenario will provide the minimum overlap between species in the two reserves. In the last section we will relax this neutral assumption.

Let's take a number s_1 of different species randomly from the n species pool to occupy the first reserve. For the second reserve we must choose randomly s_2 different species from the pool. We can now imagine that the pool has been divided in two urns: the first with s_1 species and the second with $n - s_1$ different species. We will compute the probability q_m that, after taking s_2 random species, m of them were actually present in the first urn. q_m is thus the probability of having an overlap of m common species between the two reserves.

The s_2 species group will be constituted by m species from the urn with s_1 species and $s_2 - m$ from the urn with $n - s_1$ species. There are $\binom{s_1}{m}$ different, even possibilities of choosing m species from the first urn. Similarly, there are $\binom{n - s_1}{s_2 - m}$ different, even ways of choosing $s_2 - m$ species from the second urn. Having in mind that every choice is independent, that we assume a uniform probability distribution of colonization, and that the total number of choices is $\binom{n}{s_2}$, the probability q_m of having m common species is given by the hypergeometric distribution:

$$q_m = \frac{\binom{s_1}{m}\binom{n - s_1}{s_2 - m}}{\binom{n}{s_2}}, \tag{5}$$

where, if $s_2 \geqslant s_1$, $m = 0, 1, 2, \ldots, s_1$; and if $s_2 \leqslant s_1$, $m = 0, 1, 2, \ldots, s_2$.

The mean species overlap between both reserves is determined by the mean of the hypergeometric distribution:

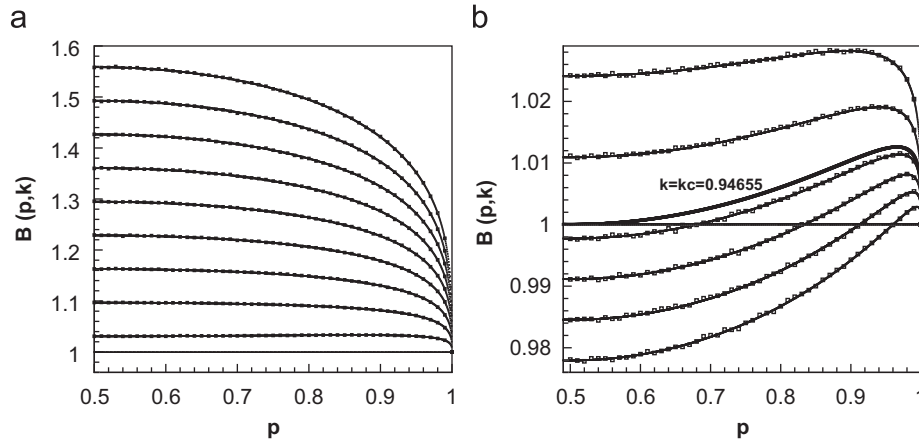$$\langle q \rangle = \frac{s_1 s_2}{n}, \tag{6}$$

Fig. 1. Relative biodiversity $B(p,k)$ versus relative reserve size p between two reserves for different values of the local-to-regional species richness ratio k: (a) $k = 0.1, 0.2, \ldots, 0.9$ from top to bottom; and (b) $k = 0.91, 0.93, 0.95, 0.96, 0.97$, and 0.98 from top to bottom. Dots represent numerical simulations (average over 100 realizations, where the regional pool is $n = 10000$ species), and lines depict the theoretical equation (9). (a) $B(p,k) > 1$ Indicating that it is always better to choose two reserves to maximize biodiversity. (b) When $k > k_c \approx 0.947$, choosing one or two reserves will depend on p: for low to moderate values of p, $B(p,k) < 1$ indicating that the best option is now choosing only one reserve. Note also that for values of k below $k_t \approx 0.862$, two identical reserves ($p = 0.5$) gives the maximum biodiversity for all k, but beyond this threshold, $p = 0.5$ changes from a maximum to a minimum of biodiversity. This situation can be easily understood by looking at Fig. 3; $z = 0.3$.

We are interested in maximizing biodiversity. Therefore, we need to maximize the following function (Higgs and Usher, 1980):

$$F(p,s,n) = s_1 + s_2 - \langle q \rangle = s_1 + s_2 - \frac{s_1 s_2}{n}. \qquad (7)$$

Taking into account the species–area relationship (1, 2, 3), biodiversity is given by

$$F(p,s,n) = s[p^z + (1-p)^z] - \frac{s^2}{n} p^z (1-p)^z. \qquad (8)$$

Let us define the ratio $k = s/n$, where once more s is the number of species supported by a single reserve of total area A (1), and n is the regional species pool. k is thus a local-to-regional species richness ratio; small k-values indicate rich continents, diverse taxons, and/or a small protected area. If we now divide Eq. (8) by s, we can define an index of relative biodiversity $B(p,k)$:

$$B(p,k) \equiv \frac{F(p,k)}{s} = p^z + (1-p)^z - kp^z(1-p)^z, \qquad (9)$$

The solution $B(p,k) = 1$ defines a critical line in such a way that for $B(p,k) > 1$, having two small reserves maximizes biodiversity, whereas if $B(p,k) < 1$, having only one reserve is the best option. Note that, as long as the species pool n is larger than s, $0 < k = s/n \leqslant 1$ so as a fact of symmetry, we only have to consider the situation $0.5 \leqslant p \leqslant 1$.

The behavior of $B(p,k)$ for several values of k is plotted in Fig. 1. Hereafter we assume without lack of generality $z = 0.3$. Note that for values of k between 0.1 and 0.9 (Fig. 1a), the relative biodiversity $B(p,k)$ is always larger than 1. This means that regardless of the reserve size distribution p, it is always better to have two small reserves than a big one.

Above some critical value $k_c = 0.94655\ldots$, choosing one or two reserves depends strongly on the size distribution p
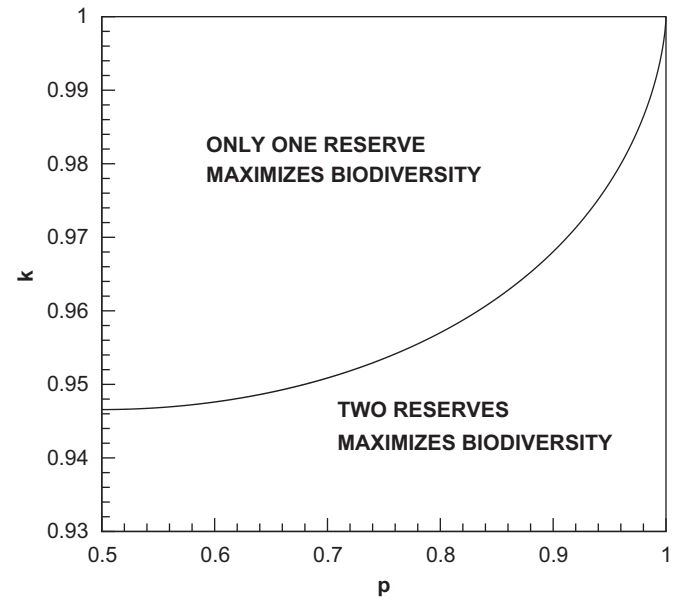

Fig. 2. The isocline $B(p,k) = 1$ in the space $p - k$ separates the regions where the optimal choice in order to maximize biodiversity is either one reserve or two reserves.

(see Fig. 1b). For low p-values, one reserve is better ($B(p,k) < 1$), but after a large enough p-value, two reserves maximize biodiversity as before ($B(p,k) > 1$). k_c can be derived easily by solving $B(p,k)|_{p=1/2} = 1$.

The above results are summarized in Fig. 2, where the isocline $B(p,k) = 1$ is plotted in the space $p - k$. Points (p,k) below the critical line indicate situations in which two reserves maximize biodiversity.

k does not only determine whether one or two reserves maximize biodiversity through the critical k_c value explored above. Within the domain of two reserves, there

is another critical k value (k_t) that determines the optimum size allocation between the two reserves. Note in Fig. 1a that for every value of $k \leqslant 0.8$, relative biodiversity reaches its maximum when $p = 0.5$, that is, for two reserves of the same size. However, for $k \geqslant 0.91$, $p = 0.5$ still represents an extrema of the biodiversity index, but has changed from maximum to minimum (Fig. 1b). The maximum relative biodiversity is now associated to higher values of p. All these conclusions can be derived in detail from the extrema analysis of $B(p, k)$. In order to find directional extrema $(p, k)^*$ of $B(p, k)$, we fix k. This converts $B(p, k)$ into a parametric function of k, say B_k. We then solve:

$$\frac{\partial B_k(p)}{\partial p} = 0. \tag{10}$$

A first solution of this equation is $p = 0.5 \ \forall k$. Now we tackle the second derivative, which gives information both on the function's convexity and on the nature of the extrema. Now we can evaluate for which value of $k = k_t$, the size allocation $p = 0.5$ changes from maximum to minimum. That is

$$\left. \frac{\partial^2 B_k}{\partial p^2} \right|_{p=1/2} = 0. \tag{11}$$

The solution to this equation is

$$k_t = (1 - z)2^z, \tag{12}$$

that in our case ($z = 0.3$) is $k_t \simeq 0.862$. This is the threshold that distinguishes the domain where $p = 0.5$ represents either a maximum or a minimum of biodiversity. In Fig. 3 we represent the extrema $(p, k)^*$ of $B(p, k)$. We can clearly observe the extrema bifurcation: under k_t, $p = 0.5$ (two
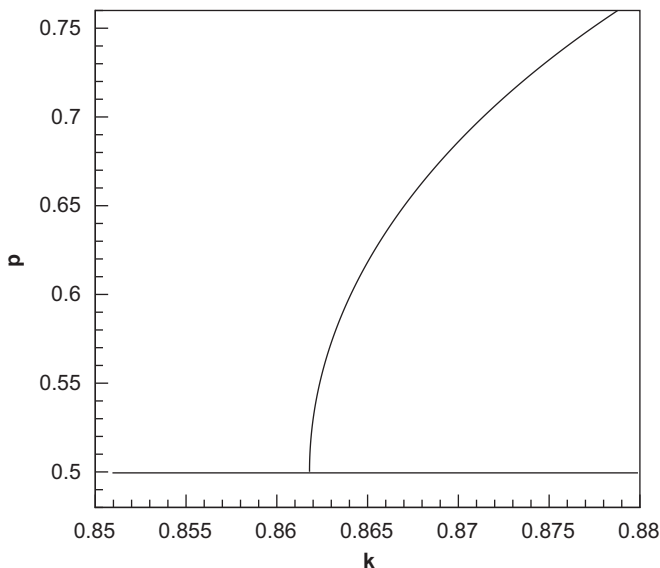

Fig. 3. Extrema (k, p) of the relative biodiversity function $B(p, k)$. Note that at the threshold $k_t \approx 0.862$ an extrema bifurcation takes place. Below this threshold, $p = 0.5$ is a maximum of $B(p, k)$. Above it, $p = 0.5$ converts into a minimum of $B(p, k)$, and a new maximum of $B(p, k)$ appears for $p > 0.5$. This maximum strongly depends on p.

reserves of the same size) maximizes the function. This extrema turns into a minimum above k_t, and a new maximum appears with $p > 0.5$ (favoring an asymmetric distribution of reserves).

3. Generalization to r reserves

The problem can be generalized from two reserves to a generic number r. The argument is as follows:

First, suppose again that we can determine the area distribution of the reserves, so that the area of the ith reserve will be $A_i = p_i A$ (with $A = \sum_{i=1}^m p_i A$). Then, for each reserve i, we have

$$s_i = cA^z p_i^z = sp_i^z, \tag{13}$$

where again, $s = cA^z$.

If we have only one reserve, the function that we should maximize will be, trivially, the constant function $F_1 = s_1$. We have just seen that in the case of two reserves, we could divide the pool in two urns, one with s_1 species and the other one with $n - s_1$. This fact leads us to maximize the function $F_2 = F(p, s, n) = s_1 + s_2 - (s_1 s_2/n)$ giving the total number of different species in both reserves.

In the case of three reserves, we can repeat the process of dividing the pool in two urns: now the first urn will contain F_2 different species and the other one $n - F_2$. Reasoning as before, we would obtain a new function $F_3 = F_2 + s_3 - (F_2 s_3/n)$. We can generalize for r reserves through the following recurrence equation:

$$F_r = F_{r-1} + s_r - \frac{F_{r-1} s_r}{n}. \tag{14}$$

It is easy to demonstrate by induction that

$$F_r = n \left\{ 1 - \prod_{i=1}^r \left(1 - \frac{s_i}{n} \right) \right\}. \tag{15}$$

Using the species–area relationship (1), defining again $k = s/n$ and dividing it by s, we find a generalized expression for the relative biodiversity:

$$B_r(\{p_i\}, k) \equiv \frac{F_r}{s} = \frac{1}{k} \left\{ 1 - \prod_{i=1}^r \left(1 - kp_i^z \right) \right\}. \tag{16}$$

Thus, the problem now becomes a search of the area distribution $\{p_i\}$ that maximizes $B_r(\{p_i\}, k)$. This corresponds to minimizing the following function:

$$G_r(\{x_i\}) = \prod_{i=1}^r (1 - x_i^z), \tag{17}$$

for $i = 1, \dots, r$, where we have defined the variables x_i such that $x_i = k^{1/z} p_i$.

We use the Lagrange multipliers method to perform this task. As long as the logarithmic operator is a monotonically increasing function, the minimum of G_r will coincide with the minimum of $\log(G_r)$. Applying this

transformation:

$$\log G_r(\{x_i\}) = \sum_{i=1}^{r} \log(1 - x_i^z), \tag{18}$$

will be the function to minimize. Note that

$$\sum_{i=1}^{r} x_i = \sum_{i=1}^{r} k^{1/z} p_i = k^{1/z} \sum_{i=1}^{r} p_i = k^{1/z}, \tag{19}$$

so that we can write the Lagrangian associated to (18) as

$$\mathscr{L} = \sum_{i=1}^{r} \log(1 - x_i^z) - \lambda \left[\sum_{i=1}^{r} x_i - k^{1/z} \right]. \tag{20}$$

Solving the system and undoing the changes to x_i we get

$$\lambda = \frac{p_1^{z-1}}{k p_1^z - 1} = \cdots = \frac{p_i^{z-1}}{k p_i^z - 1} = \cdots = \frac{p_r^{z-1}}{k p_r^z - 1}. \tag{21}$$

A trivial solution is the uniform distribution:

$$p_1 = \cdots = p_i = \cdots = p_r = \frac{1}{r}. \tag{22}$$

A second solution is

$$p_1 = p,$$
$$p_i = \frac{1-p}{r-1}, \quad i = 2, \ldots, r. \tag{23}$$

Note that when $r = 2$ we get our previous results. In fact, if we fix $r = 2$ in (21), we get Eq. (10) as expected (the solution of Lagrange multipliers gives us the extrema).

Again, if we set $r > 2$, we have that the uniform distribution (22) acts as a maximum until a critical value k_t is reached, from which it acts as a minimum, letting distribution (23) act as the maximum.

From now on we will focus on the uniform case, where (22) maximizes biodiversity. Starting from Eq. (16) and assuming a uniform distribution (22) of reserve sizes, the relative biodiversity will be

$$B_r(p, k) = \frac{1}{k} \left\{ 1 - \left(1 - \frac{k}{r^z} \right)^r \right\}. \tag{24}$$

As in the case of $r = 2$, we have to check that this distribution maximizes biodiversity until some threshold k_t (that is, that this distribution, being an extrema of $B_r(p, k)$, changes from maximum to minimum). For this, we have to solve $H_r = (h_{ij})_{r \times r}$, the Hessian of $B_r(p, k)$, fixing k and assuming $p = 1/r$. Thus, the diagonal terms of the Hessian will be

$$h_{ii} = \frac{z(z-1)}{r^{z-2}} \left(1 - \frac{1}{r^z} \right)^{r-1} \equiv a, \tag{25}$$

and the non-diagonal terms

$$h_{ij} = \frac{-z^2 k}{r^{2z-2}} \left(1 - \frac{1}{r^z} \right)^{r-2} \equiv b. \tag{26}$$

Note that when we set $r = 2$, the conditions under which $p = 1/r$ represents a maximum of biodiversity are $h_{11} < 0$

and $|H_2| > 0$. Solving this set of inequalities, we find again the expected solution $k < k_t = (1 - z)2^z$.

In the general case $r > 2$, we proceed as follows:

The first condition is $h_{ii} < 0$, which is satisfied trivially $\forall r$. The second condition is that the determinant of the Hessian changes from positive to negative at some value k_t. That is, we need to find k_t that satisfies $|H_r| = 0$. To solve the determinant of an r-order matrix is in general a tough problem. However, due to the fact that the determinant is an algebraic invariant, we just have to diagonalize the Hessian, and ask when any eigenvalue becomes null. As a fact of symmetry, we find that the Hessian has the following shape:

$$H_r = \begin{pmatrix} a & b & b & \cdots & b \\ b & a & b & \cdots & b \\ b & b & a & \cdots & \cdots \\ \cdots & \cdots & b & a & b \\ b & \cdots & \cdots & b & a \end{pmatrix},$$

which is a circulant matrix $r \times r$ with r eigenvalues:

$$\lambda_1 = a - b \quad \text{with multiplicity } \sigma(\lambda_1) = r - 1,$$
$$\lambda_2 = a + (j - 1)b \quad \text{with multiplicity } \sigma(\lambda_2) = 1.$$

Hence, $|H_r| = 0$ provides two solutions depending on whether $a = b$ or $a = (1 - r)b$.

The first possibility gives us a mathematical solution with $k_t > 1$, which has no physical meaning. The second possibility gives us the relation:

$$k_t = \frac{r^z(z - 1)}{z(2 - r) - 1}, \tag{27}$$

which is on good agreement with the case $r = 2$ and is the general solution of the problem. We can conclude that in the case of r reserves, the size distribution $p = 1/r$ maximizes biodiversity as long as the local-to-regional species richness ratio k is lower than the critical value k_t. Beyond this threshold and as a fact of consistency, the size distribution that will maximize biodiversity will be the other extreme found in (23).

4. Relaxing the neutral assumption

Up to here we have assumed neutrality, i.e., that all species have the same colonization probability. This allowed analytic tractability. In order to see how robust previous results are in the face of relaxing neutrality, we will now present numerical results for the general case with a more realistic colonization probability distribution.

Finding an analytical expression of the distribution overlap similar to Eq. (5) is a difficult problem when the colonization probability distribution is no longer uniform, but a power law (Eq. (4)). However, we are only interested in the mean of that distribution, i.e., the mean overlap. We can assume, for a fixed k, the following ansatz for the mean
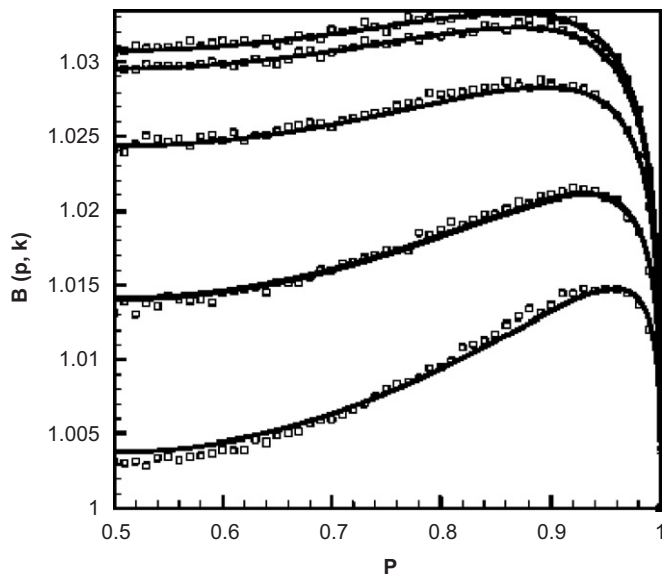
Fig. 4. Similar to Fig. 1 but for r reserves and different colonization probability distributions described by values of γ in Eq. (4). Squares represent Monte Carlo simulations and lines represent the ansatz (28). $k = 0.9$, and from top to bottom, $\gamma = 0$ (corresponding to the uniform probability distribution), 0.1, 0.25, 0.5, and 0.75. As noted, departing from neutrality ($\gamma = 0$) does not affect largely the analytic solution.

of that distribution:

$$\langle q \rangle = \frac{s_1 s_2}{n} P(\gamma) 2^{-\gamma}, \tag{28}$$

where $P(\gamma)$ is a polynomial whose coefficients will have to be estimated through fitting. In Fig. 4 we compare some numerical results with this ansatz for the case $k = 0.9$. Note that the agreement is quite good. We find as the best fitting for $P(\gamma)$ a second order polynomial of the following shape: $P(\gamma) \approx 1.0 + 0.7\gamma + 0.41\gamma^2$. Unfortunately, we have not found a general simple ansatz so that this polynomial must be fitted for each value of k.

The numerical results shown in Fig. 4 clearly illustrate that for values of $\gamma < 1$, the species-specific colonization probabilities reduce relative biodiversity by less than 3%.

5. Discussion

We have developed a probabilistic framework to optimum reserve design. It dictates the optimum size allocation among a set of r reserves. We have found that a simple variable k depending on the area allocated to reserves and the regional species richness is a key determinant of the best size distribution. For high regional species richness and low reserve areas, a uniform area distribution maximizes biodiversity. For low regional species richness and high reserve areas, the optimum size allocation consists of allocating a certain area to one reserve and uniformly distributing the remaining area among the remaining reserves.

Recent research has linked the species–area relationship with two other independently derived power laws in

ecology (Southwood et al., 2006), namely species frequency versus species length, and maximum body size versus area. Here we add to this work by showing yet another relationship of the species–area exponent z. Interestingly enough, the critical value k_t separating the two optimum reserve size allocation is determined by the number of reserves raised to the power-law exponent of the specie-s–area relationship (see Eq. (27)). This connection between identical variables sets up the possibility of extending some of the current findings in the context of other ecological laws. For example, the commonly observed value of the exponent z is related to the underlying lognormal species abundance distribution (Southwood et al., 2006; García Martín and Goldenfeld, 2006), and thus one could explore how species abundance distributions may affect optimum reserve design. Exponent z also depends on habitat and scale (García Martín and Goldenfeld, 2006), so despite the spatially implicit assumptions of our model, such details could be incorporated through z.

Our analytical solutions depend only on the underlying species–area relationship, which although seems to be a good descriptor of real distributions if: (i) individuals cluster in space and (ii) if abundance distribution is similar to Preston's lognormal, it is independent on specific details of these properties (García Martín and Goldenfeld, 2006). This suggests that our approach is also independent on details.

The numerical solutions in the previous section allow us to relax the neutrality assumption. Our analytic results are robust for moderate departures from neutrality. This implies that specific complexities in the colonization rates across species would probably affect only quantitatively but not qualitatively our analytic results. This suggest the value of simple, yet general analytic predictions, which despite their simplicity can be used to provide general rules of thumb.

References

Arponen, A., Heikkinen, R., Thomas, C., Moilanen, A., 2005. The value of biodiversity in reserve selection: representation, species weighting, and benefit functions. Conserv. Biol. 19, 2009–2014.

Atmar, W., Patterson, B., 1993. The measure of order and disorder in the distribution of species in fragmented habitat. Oecologia 96, 373–382.

Cabeza, M., Moilanen, A., 2003. Site-selection algorithms and habitat loss. Conserv. Biol. 17, 1402–1413.

Cook, R., Quinn, J., 1998. An evaluation of randomization models for nested species subsets analysis. Oecologia 113, 584–592.

Darlington, P., 1957. Zoogeography: The Geographical Distribution of Animals. Wiley, New York.

Fischer, J., Lindenmayer, D., 2002. Treating the nestedness temperature calculator as a ''black box'' can lead to false conclusions. Oikos 99 (1), 193–199.

García Martín, H., Goldenfeld, N., 2006. On the origin and robustness of power-law species–area relationships in ecology. Proc. Natl Acad. Sci. USA 103, 10310–10315.

Halpern, B., Regan, H., Possingham, H., McCarthy, M., 2006. Accounting for uncertainty in marine reserve design. Ecol. Lett. 9, 2–11.

Higgs, A., Usher, M., 1980. Should nature reserves be large or small? Nature 285, 568–569.

Hubbell, S., 2001. The Unified Neutral Theory of Biodiversity and Biogeography. Princeton University Press, Princeton, NJ.

MacArthur, R., Wilson, E., 1967. The Theory of Island Biogeography. Princeton University Press, Princeton, NJ.

May, R., 1975. Patterns of species abundance and diversity. In: Cody, M., Diamond, J. (Eds.), Ecology and Evolution of Communities. Harvard University Press, Cambridge, MA, pp. 81–120.

Nicholson, E., Westphal, M., Frank, K., Rocherster, W., Pressey, R., Lindenmayer, D., Possingham, H., 2006. A new methods for conservation planning for the persistence of multiple species. Ecol. Lett. 9, 1049–1060.

Patterson, B., 1987. The principle of nested subsets and its implications for biological conservation. Conserv. Biol. 1, 323–334.

Southwood, T., May, R., Sugihara, G., 2006. Observations on related ecological exponents. Proc. Natl Acad. Sci. USA 103, 6931–6933.

Williamson, M., 1988. Relationship of species number to area, distance and other variables. In: Myers, A., Giller, P. (Eds.), Analytical Biogeography. Chapman & Hall, New York, pp. 91–115.

Wilson, K., McBride, M., Bode, M., Possingham, H., 2006. Prioritizing global conservation efforts. Nature 440, 337–340.