



Spatial and biological aspects of reserve design

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The optimal spatial design of protected reserves requires attention to the biological mechanisms underlying community organization, and sustaining ecosystem services. Identifying the key mechanisms is especially difficult in species-rich ecosystems. We investigate the example of the tropical rainforest, a biome that is under threat of continuing fragmentation, yet which shelters the majority of living species on Earth. Simple dynamic and spatially explicit simulations, which model the dynamics of plant communities, allow us to elucidate the interplay between patterns of fragmentation and seed dispersal mechanisms in maintaining biodiversity.

1. Introduction

Preserving tropical rain forests has been a priority for conservation biology since the early 1970s [1], and for many good reasons. Rain forests represent a rich reservoir of biodiversity, more than 70% of tropical rainforest species being restricted to this biome. For woody plant species alone, a record-setting species richness has been found in western and central South America, with above 300 species for trees of more than 10 cm in diameter in a single hectare [2,3]. For bird species, “hotspots” were located in the Peruvian Amazon and elsewhere [4]. The geographical distribution of the biodiversity is far from homogeneous, and a significant fraction of these species are rare, specialized and/or endemic, and therefore highly sensitive to disturbances.

The preservation of tropical forest biodiversity is an ethical, political and practical concern. The world’s annual consumption of wood products was estimated to reach 4200 million m³ in year 2000 [5]. About 55% of this consumption is used locally (mostly fuel wood) and the remaining 45% is traded. Timber wood accounts for 16% of the grand total. The European International Organization for Tropical Woods reports 220 million m³ in 1997, mostly from Brazil, Malaysia, Indonesia, and India. Timber exports represented a net income of US\$11.7 billion in 1997 for tropical countries [6]. Non-timber forest products, which have been used by local people for a long time, have been gathered by ethno-botanists [7,8], and is being exploited by the bioprospecting industry.

Poor management practices have driven the tropical rainforest to the verge of a major collapse [9]. The historical extent of this biome was 21 million km², of which 10.9 million km² (52%) remained intact in 1990. The estimated rate of deforestation is 130,000 km²/y [10]. The destruction of large expanses of forests not only increases the risk of species extinction by orders of magnitude [11], but also results in a net source of atmospheric carbon [12], which

will in turn alter biodiversity via changes in the metabolism of terrestrial ecosystems and climate change [13]. Moreover, fragmented or extensively logged rainforests experience significant shifts of species assemblages [6,14,15].

The selection of protected wildlife reserves is a powerful tool to preserve this endangered habitat [16] and to curb the current rate of tropical deforestation. A rapidly growing literature is raising and addressing practical issues related to the protection of tropical wildlands, including rainforests, at the regional scale. In this context, the development of techniques to select and design natural reserves, constrained by political, economical, environmental, and ecological factors, is a difficult but essential task [17]. Recently, strong emphasis has been placed on whether reserve selection algorithms yield mathematically optimal results [18]. However, economic and social factors may be overriding, and even more challenging to address [19,20]. This especially holds in developing countries, where efforts to install protected areas are often hampered by rapid demographic growth, social difficulties, or widespread governmental corruption.

Too often, reserve selection models assume that (a) one knows perfectly the state of the biological system at time t , (b) one can define a cost function, and (c) this function can be minimized with respect to the state of the system at time t . Beyond the observation that (a) and (b) are rarely correct, this approach disregards the future dynamics of, and biotic interactions among, these species. Inclusion of such dynamics and interactions in general alter the conclusions of static reserve selection models. This caveat is confirmed by recent studies on the selection of areas that maximize biodiversity, including criteria for persistence [21], as well as by long-term studies, which show that the choice of reserves does affect the dynamics of the ecosystem in the long run [22]. Thus, dynamical models must form the basis of reserve-design decisions.

The valuation of ecosystem services is feasible for tropical forests [17]. Moreover, practical methods are being developed to survey the diversity at the landscape-to-regional scale [23,24]. The use of these spatial data to narrow down

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high priority areas would clearly be of benefit to design techniques. In this contribution, we do not address the problem of the valuation of ecosystem services for the rain forest; for these, the reader is referred to Daily [25], and Dasgupta et al. [26] for a recent overview. Nor do we suggest specific policies for protecting the rain forest biome [27–29]. Rather, we focus on the theoretical implications of using dynamic spatial reserve design models in the framework of species-rich ecosystems. This represents an area of high priority in the development of conservation theory and practice.

2. Spatial distribution of species

We are here concerned with the protection of species-rich communities. In addition to the financial, social, and developmental problems raised by the creation of any nature preserve, at least two aspects are crucial in this special case. The species assemblage usually is of an exceptional ecological value, and the biological processes that govern this ecosystem are often only very imperfectly known. Therefore, biodiversity assessment should be a major focus in such nature preservation programs. Several methods of biodiversity assessment have been employed, ranging from transect surveys (rapid biodiversity assessment programs) and species accumulation functions [30], to the use of indicator taxa [29,31,32]. For a recent overview of these methods, the reader is referred to [33]. We simply point out that the issue of scaling-up this local information to the landscape level has been poorly addressed so far. For example, power-law species-area curves have been widely used for scaling-up to the landscape level [34, 35], despite the lack of theoretical grounds for these extrapolation techniques. In fact, large-scale censuses of plants in several vegetation types have shown that real species-area curves often strongly depart from the power-law shape [36] for plant species. Likewise, the predictive power of indicator taxa for estimating biodiversity has been challenged by the results of intensive biodiversity inventories [37].

Natural terrestrial communities are complex systems in which function, structure and composition all play important roles. These three aspects maintain natural ecosystems in a subtle and ever-changing state, whose processes are still far from being fully understood. The fragmentation of ecosystems may alter their functioning in complex ways. Several modeling approaches have been proposed to go beyond the predictions of statistical techniques to incorporate the mechanisms that promote the maintenance of species diversity. It is the purpose of the present contribution not to list or to compare these [38,39], but rather to develop a dynamic simulation approach to studying fragmentation [40]. A spatial and dynamic picture is needed to understand how these mechanisms function; for forest plant species, spatially-explicit forest growth simulators [41–43] provide a vital tool. Such individual-based models [44] are stochastic, simulating the behavior of all members of a biological population as individuals. Simplified stochastic simulators have also been

studied both numerically and analytically [45], but more detailed spatially-explicit individual-based simulation models are needed to go beyond generalities, and to help assess the reliability and predictability of spatial optimization models in a non-linear dynamic context.

3. Model

3.1. Description of the model

To illustrate our point, we use a simple, spatially-explicit model of the dynamics of a species-rich plant population. The model we choose is one developed and analyzed by Durrett and Levin [45], and is based on Hubbell's drift hypothesis [46]. We first describe Hubbell's model, then introduce Durrett and Levin's individual-based version of this model. More complex models are certainly possible, but the simple model more clearly elucidates the central lessons.

Hubbell [46] models a homogeneous forest community, i.e., with no habitat heterogeneity, by an assembly of N patches, each with one or several individuals of a given species. A dead canopy tree creates a treefall gap, which clears the patch. This vacated patch is immediately replaced by the young of one of the surviving trees, chosen at random within the remaining patches. Most seeds are not dispersed long distances, especially in the rainforest; but rare long-dispersal events are possible, for example when seeds are transported by birds, or by large mammals. In the following, we assume that a fraction D of the seeds are transported over long distances, and are redistributed uniformly in the community, whereas the rest $(1 - D)$ land in the immediate neighborhood.

During one time step, a fraction m of the sites experiences a treefall event, where m is the turnover rate. Unlike individual-based models [41], the growth of trees is not explicitly modeled; rather, we only keep track of the species identities present at a site. The model assumes that species are equivalent; that is, they have the same turnover rate (i.e., the probability for patches to be cleared is independent of the species presently inhabiting the patch), and the same competitive ability (i.e., each seed in a cleared patch has the same probability of winning the patch). Species thus compete symmetrically, with probabilistic colonization events playing a central role in determining numerical dominance within the community. Mathematical details of this model can be found in the appendix and the parameters and variables are listed in table 1.

A typical simulation is started with only one species present, and new species are added into the system at a rate ν per individual per time step (typically, $\nu = 10^{-6}$). During a transient, the simulated community accumulates species, until a "species carrying capacity" is reached. The number of species at carrying capacity, S , is a balance between the permanent input of new species, and the stochastic extinction of rare species. The immigration rate ν is very small compared with the turnover rate.

Table 1
Description of the variables and parameters used in the model.

Variable or parameter	Interpretation
N	Total number of patches
L	Linear size of the simulated community ($N = L^2$)
S	Number of species in the simulated community
v	Immigration/speciation rate (per individual per time step)
D	Fraction of globally dispersed seeds
p	Fraction of protected area
n	Number of selected square reserves
a	Linear size of one reserve

In the model described in [45], the individual nature of trees is embodied in the assumption that only one tree can occupy any cell of a square lattice of size $L \times L$. In other words, the number of patches N is equal to L^2 . This model is slightly different than Hubbell's in that it models every individual within a patch, while assuming that all individuals occupy the same size space. The turnover rate therefore is equivalent to the individual's death rate. Durrett and Levin show that these two models are equivalent with respect to the community-scale features. The diversity of organisms (plants, animals and microbes) other than trees is not explicitly modeled, but we make the assumption that the total diversity of our ecosystem is correlated with the tree diversity S .

Chave et al. [47] have analyzed in detail the spatial patterns of plant species richness emerging from Durrett and Levin's version of Hubbell's model. In particular, they find that, under limited dispersal, the species-area curve (number of species in nested subplots as a function of the subplot area) fits a power law; while under global dispersal, it has a logarithmic shape (the number of species increases as the logarithm of the sampled area).

3.2. Model dynamics and fragmentation

All simulations were started after the immigration-extinction equilibrium was reached. Therefore, our initial state is a pristine rain forest, carrying maximal species diversity. We then imposed different environmental disturbances on our theoretical ecosystem. Some areas of forest were perfectly protected, whereas other areas completely destroyed. This type of disturbance is relevant to many cases of forest fragmentation, be it due to intensive logging, cattle ranching, monocultures, or mining activities.

We varied the fragmentation intensity (number of patches destroyed), as well as the shape of the fragmented area. We denoted by p the fraction of the lattice that is to be given protected status. Static optimization models for reserve designs tend to protect several contiguous patches, in order to lower the ecological consequences of fragmentation at the community level. We reproduced these mechanisms, but we focused on the consequences for the diversity of the ecosystem rather than on ecosystem structure implications [33,48]. To construct "designed" reserves, we selected n ($< N$) patches at random around which we protected a square window of side a with the selected patch at the center. We then computed the effective protected area, which is less than na^2 , as the windows may overlap. In all the simulations, we first fixed a , then varied n such that the protected fraction p was reached. We ran the model in this configuration (figure 1).

Seed dispersal plays a crucial role with respect to the stability of the fragmented ecosystem. On the one hand, one may want to provide linkages between patches, in order to prevent a given species from going extinct, and to avoid genetic bottlenecks. However, too much synchrony across the plots may have a negative impact too [49]. Here we have used our patch-based model to assess the relative impact of fragmentation on dispersal. We have made use of the null-model of fragmentation, which assumes that patches are re-

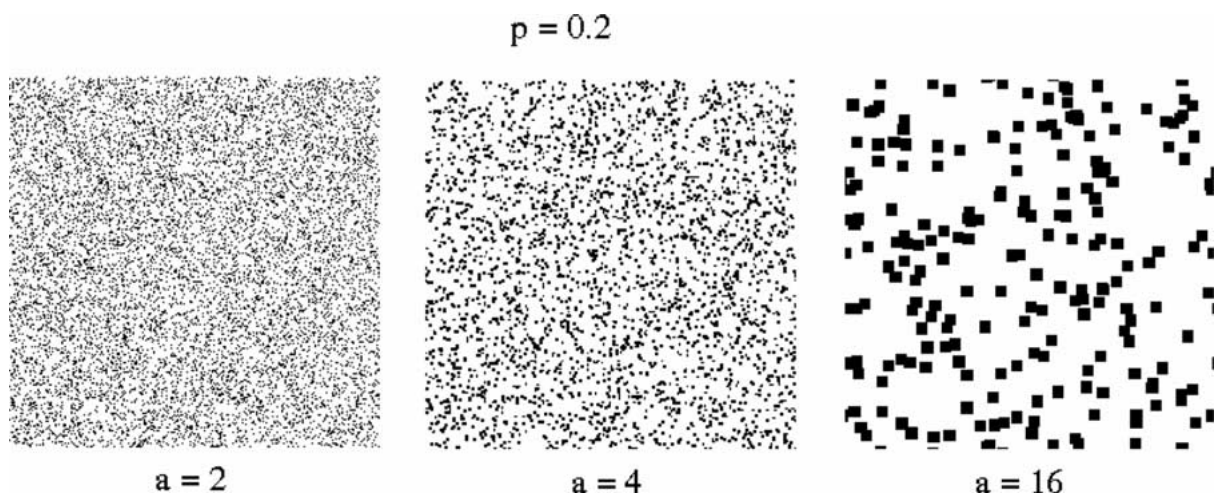


Figure 1. Correlated reserve design on a landscape of size 512×512 for a high degree of fragmentation ($p = 0.2$). Reserves are assumed to have a square shape of side 2, 4 and 16.

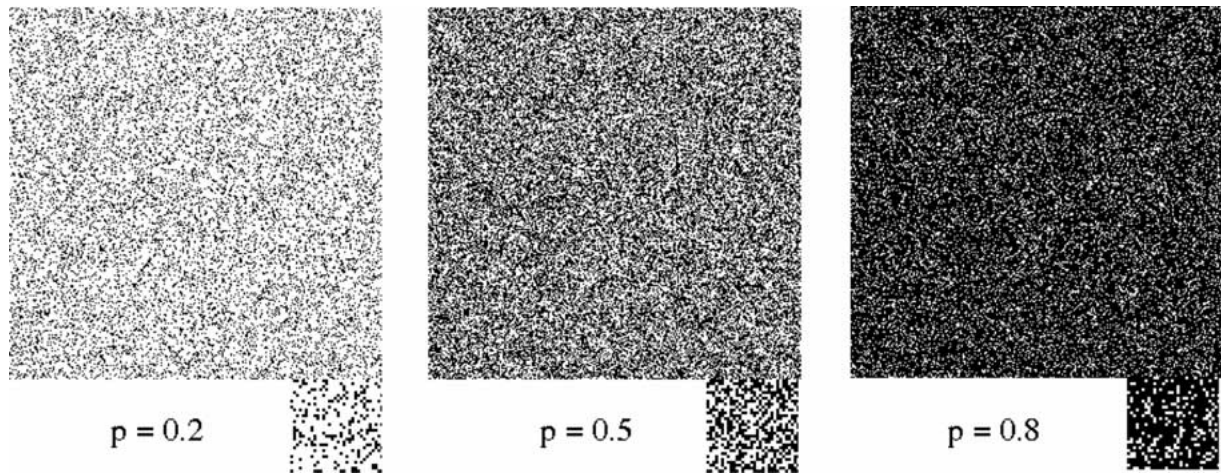


Figure 2. Random reserve design on a landscape of size 512×512 for three values of p . Insets: magnification 4 times.

moved independently and homogeneously across the landscape (figure 2).

We performed runs in the following way. First, we constructed a basic environment landscape, with some patches allowed and some forbidden, according to one of the two described designs (correlated or random), and then superimposed vegetation dynamics upon it. We simulated a system of 512×512 patches, each supporting at most one plant species. We insured that the system always reached an equilibrium in the number of species.

4. Results

4.1. Long-term equilibrium of a designed reserve

We require that our simulated forest be protected in a number of identical-sized patches of continuous forest. We have constructed such a design by selecting, at random, n squares of side a . For $a = 1$ and $n = pN$, windows around the patches are of size zero, and thus we are in the random fragmentation case. When na^2 is of the order of N , almost all of the patches are protected (actually, if $N = na^2$, $p = 1 - 1/e \approx 63\%$ of the forest is protected since the squares are randomly placed). For the purpose of this study, we fixed the fraction of long-distance dispersed seeds to $D = 0.1$, and we varied n and a . For a , we took the values 2, 4, 16 and 64 in a matrix of size 512×512 . The system was run to equilibrium in all cases.

Not surprisingly, the total number of species always increased as the area given protected status increased (figure 3). This feature is consistent with observed patterns [50]. When the entire system was protected ($n = N$), 160–180 species could be packed into the environment, assuming an unlimited species pool for the model. It should be noticed that the number of species did not increase linearly with the fraction of protected land, indicating the crucial importance of biological interactions for the process of species protection.

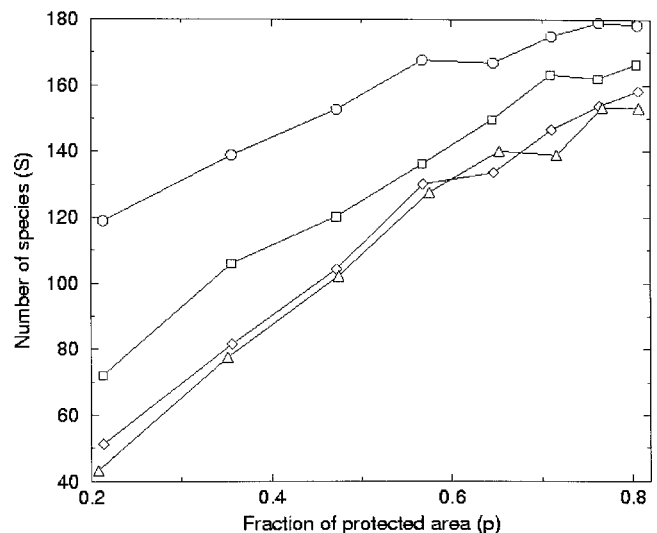


Figure 3. Total number of species in a system with correlated fragmentation. The fraction of long-distance dispersal was set to 0.2. The four curves represent different degrees of correlation, $a = (\circ)$ 2, (\square) 4, (\diamond) 16 and (\triangle) 64. Each point was obtained by replicating 10 systems of side 512.

For a fixed fraction of the protected area, p , the number of species depended on the reserve design. A large number of small reserves appeared to protect the species more efficiently than a few large reserves. For example, with reserves of size 2×2 , only 20% of protected land sheltered 67% of the species of the undisturbed landscape (around 180 species), while for reserves of size 64, the remaining diversity was only 27%. In small sized reserves, biological interspecific interactions are much less important. If a large number of small-sized and isolated remnants occupy the system, e.g., if there is no possible dispersal across them, the number of species is given by the number of such remnants. Here, we refer to as “isolated” remnants that cannot receive offspring from neighboring preserves. Such a situation is achieved under nearest neighbor dispersal and for a relatively high fraction of disturbed patches. At the species level, there is a

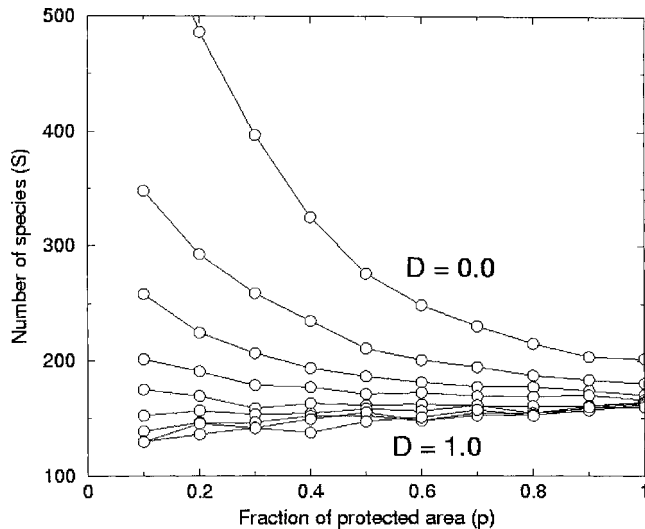


Figure 4. Total number of species in a system with random fragmentation. Two parameters were varied during this computer experiment: the protected area p and the fraction of long distance dispersal D . Both parameters were varied between 0.1 and 1.0 with intervals of length 0.1 (a total of 100 experiments) on a square lattice of side 512. Each experiment was replicated 20 times to improve the statistics. To reach an equilibrium, the simulation was run for 40,000–80,000 time steps.

tradeoff between the area over which the species can spread, and the number of possible competitors for this area. Note that at this stage the issue of the resiliency of an ecosystem to disturbances is not yet addressed.

4.2. Seed dispersal and the impact of corridors

When a fraction of seeds are allowed to cross disturbed areas, the diversity should be significantly lower, since monospecific “islands” of vegetation now are subject to a certain amount of competition. The effect that we want to model here is the influence of corridors among small reserves scattered across a landscape (see [51] for a recent review on corridors). Therefore, we expect the system to display a wide array of dynamics as the two parameters, fragmentation fraction and dispersal distance, are varied.

Figure 4 shows the number of species obtained in a simulated community when the fraction of protected patches, as well as the fraction of offspring dispersed far from the source, are varied. If an offspring lands on a non preserved patch, it cannot survive. For a highly fragmented landscape and short-distance dispersal only, the diversity that can be maintained is high (figure 4). With many isolated remnants (figure 5), the landscape can pack a maximal number of species. For nonfragmented landscapes, competition is stronger and the number of species decreases (figure 4). We also observed a decrease of the number of species for a fixed value of the protected area, as the fraction of long-distance dispersal was increased. Long distance dispersal could be promoted by installing corridors across remnants in the landscape. One sees, then, that the corridor strategy can have a negative impact in this scenario.

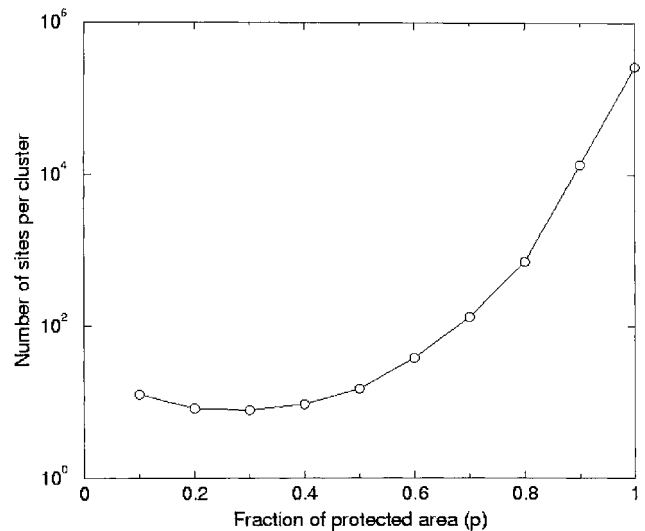


Figure 5. Number of sites per cluster (i.e., isolated remnant), under the random fragmentation algorithm. Note the logarithmic scale on the y axis. Isolated fragments were enumerated on the same lattice as in figure 2 for various values of the fragmentation parameter p . In the absence of fragmentation ($p = 1$), this there is only one cluster.

On the other hand, if a sufficient fraction of the offspring is sent far away, then the spatial arrangement of forest remnants is less important, for every cluster can be reached by the seed rain of other remnants. In this case, the total size of the protected area is the main determinant of the number of species that can be maintained in the ecological community. In particular, as the fraction of protected patches p increases, S also increases (figure 4).

5. Discussion

Fragmented landscapes are becoming more and more common in the tropical zone, because of the impact of human activities. A recent analysis of remote sensing images shows that only a third of the forest of South America, overwhelmingly dominated by the lowland tropical rain forest biome, is more than 1 km from a boundary [52].

Our results illustrate the fundamental importance of biological dynamics, such as interspecific competition and seed dispersal, in the issue of forest preservation. Understanding the mechanisms at play in an ecosystem is certainly a challenging goal, and one that cannot be overlooked. Here, we have provided a worked out example where the maintenance of diversity is explicitly modeled under the assumption of the equivalence of all species in the system (Hubbell's drift hypothesis). Real communities are much more complex regarding the mechanisms sustaining diversity [39], and further research is needed to account for more subtle modes of competition. The key point, however is that failure to represent adequately the functioning of a natural community, may lead to unsuitable, or even to harmful, management practices.

Some species must displace others to establish themselves and survive. This is achieved through direct compe-

tition or through competition for resources. The fraction of available space is then crucial, and clearly large expanses of undisturbed habitat are necessary to prevent rare species from going extinct at much larger rates than in the control scenario of a perfectly protected landscape.

Seed dispersal also plays a crucial role in the stability of the fragmented ecosystem. On the one hand, one may want to design corridors to prevent a given species going extinct, and to avoid genetic bottlenecks. However, too much synchrony across the plots may also have a negative impact. In unfragmented landscapes, the effect of this synchrony are balanced by demographic stochasticity induced by large population sizes. This contrasts with fragmented landscapes in which only a small number of individuals can coexist, and where synchrony can have a negative impact. Earn et al. [49] have recently used a model ecosystem to show that such dynamically-driven synchronous effects could drive an ecosystem to a rapid collapse. Here we have investigated this issue in the framework of our patch-based model. Although our model does not assume that populations are fluctuating chaotically in abundance, we still find that coherence in space can have a negative impact on the overall dynamics of the ecosystem.

The importance of long-term interspecific interactions is by no means restricted to the rainforest. In fact, most natural communities, including temperate grasslands and even deserts are shaped by these biotic interactions, as well as by external physical factors. We have used the tropical rain forest as an illustration of our model, because it is a critically endangered biome and because biological interactions are believed to be of fundamental importance for its stability. At the same time, models of rain forest growth have lacked a spatially explicit description until quite recently [43,48,53]. The present model builds upon this previous knowledge. It includes the notion of taxonomic species diversity, which is lacking in most in forest growth simulators, and it addresses the issue of forest matrix fragmentation [48].

Biological interactions add a major complication to the projection into the future of multi-species assemblages, based on an inventory conducted at a single point in time. Searching to optimize only a few factors to design natural reserve is pointless if essential biological factors are overlooked.

A vegetation model alone does not account for the entire diversity that one may want to protect in preserves. Most simply, one might assume a correlation between plant and animal taxa, as is practically done in diversity assessments [31]. At the other extreme, we could develop an individual-based simulation of animal populations, which would incorporate explicit interactions with the forest matrix. These might include grazing, animal-induced seed dispersal, and habitat specialization. It would be obviously desirable to have such a modeling approach available (especially for the treatment of rare species), while recognizing that complex coupled models do not always clarify the underlying mechanisms, as discussed in [54]. Our position in the present paper is pragmatic. On the one hand, we as-

sume that the floral diversity provides a good indicator of the overall diversity of the community. On the other hand, the influence of animals as seed dispersers is taken into account though the possibility of varying the number of long-distance dispersal events across the landscape.

In conclusion, the issues related to the selection of natural reserves are very different in temperate countries, mostly developed and industrialized, as compared to tropical countries. The former perceive the protection of the few remaining areas of wildlife as an ecosystem service, often promoted by tourism, and ecological research is usually incorporated in operational projects. Tropical forests of the South, however, mostly exist within difficult political and economic contexts. Most tropical rainforests certainly are essential reservoirs of biodiversity on the Earth, but environmental policies should also strive to foster compatible uses of the forest. Efficient protection of these ecosystems can only be achieved if the processes that govern their dynamics are carefully studied before irreversible decisions are taken.

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Appendix

The model used in this work is a stochastic cellular automaton defined on a square lattice of size $L \times L$. Let us first consider a nonfragmented landscape. The neighborhood N_x of any site x varies between four cells (four nearest neighbors) to all the cells of the lattice (L^2 neighbors). In our version of the model, the four nearest neighbor sites are chosen as neighbors with probability $1 - D$, while all the other sites are chosen with probability D . The two extreme cases of nearest neighbor dispersal and global dispersal are recovered when $D = 0$ and 1, respectively. With probability m , and irrespective of the occupant of site x at time t , the site is invaded by an offspring of the occupant of site y , where y is a neighboring site of x , chosen according to the above mentioned rules of dispersal. With probability v and every time step, an individual can be replaced by an individual of a new species.

In a fragmented landscape, a given fraction of patches is unsuitable for the establishment of trees. Therefore an isolated patch, made of only one tree and far from the other remnants, is at a high risk of being emptied. The dynamic rule is the same than for a nonfragmented landscape, except that only the remnants contribute to the dynamics.

References

- [1] A. Gomez-Pompa, C. Vasquez-Yanes and S. Guevara, The tropical rainforest: A non-renewable resource, *Science* 177 (1972) 762–765.
- [2] A.H. Gentry, Tree species richness of upper amazonian forests, *Proceedings of the National Academy of Sciences (USA)* 85 (1988) 156–159.
- [3] H. ter Steege, D. Sabatier, H. Castellanos, T. van Andel, J. Duivenvoorden, A.A. de Oliveira, R. Ek, R. Lilwah, P. Maas and S. Mori, An analysis of floristic composition and diversity of the Amazonian forests including those of the Guiana Shield, *Journal of Tropical Ecology* 16 (2000) 801–828.
- [4] J. Fjelds  and C. Rahbek, Species richness and endemism in South American birds: Implications for the design of networks of nature reserve, in: *Tropical Forest Remnants – Ecology, Management, and Conservation of Fragmented Communities*, eds. W.F. Laurence and R.O. Bierregaard, Jr. (The University of Chicago Press, Chicago, 1997) pp. 466–482.
- [5] World Bank, *World Development Report 1994* (World Bank, Washington, DC, 1995).
- [6] A. Grieser Johns, *Timber Production and Biodiversity Conservation in Tropical Rain Forests*, Cambridge Studies in Applied Ecology and Resource Management (Cambridge University Press, 1997) p. 225.
- [7] J.A. Duke, Tropical botanical extractives, in: *Sustainable Harvest and Marketing of Rain Forest Products*, eds. M. Plotkin and L. Famolare (Island Press, Washington, DC, 1992) pp. 53–62.
- [8] O. Phillips, A.H. Gentry, C. Reynel, P. Wilkin and B.C. G lvez-Durand, Quantitative ethnobotany and Amazonian conservation, *Conservation Biology* 8 (1994) 225–248.
- [9] S.L. Pimm and J.H. Lawton, Planning for biodiversity, *Science* 279 (1998) 2068–2069.
- [10] FAO, *State of the World's Forests* (Food and Agriculture Organization, Rome, 1997).
- [11] J.B. Hughes, G.C. Daily and P.R. Ehrlich, Population diversity: Its extent and extinction, *Science* 278 (1996) 689–692.
- [12] R.A. Houghton, D.L. Skole, C.A. Nobre, J.L. Hackler, K.T. Lawrence and W.H. Chomentowski, Annual fluxes of carbon from deforestation and regrowth in the Brazilian Amazon, *Nature* 403 (2000) 301–304.
- [13] C. K rner, Biosphere responses to CO₂ enrichment, *Ecological Applications* 10 (2000) 1590–1619.
- [14] A. Cutler, Nested faunas and extinction in fragmented habitats, *Conservation Biology* 5 (1991) 496–505.
- [15] W.F. Laurence and R.O. Bierregaard, Jr. (eds.), Species richness and endemism in South American birds: Implications for the design of networks of nature reserve, in: *Tropical Forest Remnants – Ecology, Management, and Conservation of Fragmented Communities* (The University of Chicago Press, Chicago, 1997) pp. 466–482.
- [16] M.A. Clemens, C.S. ReVelle and J.C. Williams, Reserve design for species preservation, *European Journal of Operational Research* 112 (1999) 273–283.
- [17] C. Kremen, J.O. Niles, M.G. Dalton, G.C. Daily, P.R. Ehrlich, J.P. Fay, D. Grewal and R.P. Guillery, Economic incentives for rain forest conservation across scales, *Science* 288 (2000) 1828–1832.
- [18] L.G. Underhill, Optimal and suboptimal reserve selection algorithms, *Biological Conservation* 70 (1994) 85–87.
- [19] R.L. Pressey, H.P. Possingham and C.R. Margules, Optimality in reserve selection algorithms: When does it matter and how much?, *Biological Conservation* 76 (1996) 259–267.
- [20] J.R. Prendergast, R.M. Quinn and J.H. Lawton, The gaps between theory and practice in selecting nature reserves, *Conservation Biology* 13 (1999) 484–492.
- [21] P.H. Williams and M.B. Araujo, Using probability of persistence to identify important areas for biodiversity conservation, *Proceedings of the Royal Society of London B* 267 (2000) 1959–1966.
- [22] K.M. Virolainen, T. Virola, J. Suhonen, M. Kuitunen, A. Lammi and P. Siikam ki, Selecting networks of nature reserves: Models do affect the long-term outcome, *Proceedings of the Royal Society of London B* 266 (1999) 1141–1146.
- [23] H. Tuomisto, What satellite imagery and large-scale field studies can tell about biodiversity patterns in Amazonian forests, *Annals of the Missouri Botanical Garden* 85 (1998) 48–62.
- [24] D.A. Clark, Deciphering landscape mosaics of neotropical trees: GIS and systematic sampling provide new views of tropical rainforest diversity, *Annals of the Missouri Botanical Garden* 85 (1998) 18–33.
- [25] G. Daily (ed.), *Nature's Services. Societal Dependence on Natural Ecosystems* (Island Press, Washington DC, 1997) pp. 392.
- [26] P. Dasgupta, S. Levin and J. Lubchenco, Economic pathways to ecological sustainability, *BioScience* 50 (2000) 339–345.
- [27] J. Terborgh and B. Winter, A method for siting parks and reserves with special reference to Colombia and Ecuador, *Biological Conservation* 27 (1983) 45–58.
- [28] A.E. Lugo, Management of tropical biodiversity, *Ecological Applications* 5 (1995) 956–961.
- [29] S. Keel, A.H. Gentry and L. Spinzi, Using vegetation analysis to facilitate the selection of conservation sites in eastern Paraguay, *Conservation Biology* 7 (1993) 66–75.
- [30] M.J. Sober n and B.J. Llorente, The use of species accumulation functions for the prediction of species richness, *Conservation Biology* 7 (1993) 480–488.
- [31] C. Kremen, Assessing the indicator properties of species assemblages for natural areas monitoring, *Ecological Applications* 2 (1992) 203–217.
- [32] D.L. Pearson and S.S. Carroll, Global patterns of species richness: Spatial models for conservation planning using bioindicator and precipitation data, *Conservation Biology* 12 (1998) 809–821.
- [33] D.B. Lindenmayer, C.R. Margules and D.B. Botkin, Indicators of biodiversity for ecologically sustainable forest management, *Conservation Biology* 14 (2000) 941–950.
- [34] D. Simberloff, Species turnover and equilibrium island biogeography, *Science* 194 (1976) 572–578.
- [35] B.L. Zimmerman and R.O. Bierregaard, Relevance of the equilibrium theory of island biogeography and species-area relations to conservation with a case from *Journal of Biogeography* 13 (1986) 133–143.
- [36] R. Condit, S.P. Hubbell, J.V. LaFrankie, R. Sukumar, N. Manokaran, R.B. Foster and P.S. Ashton, Species-area and species-individual relationships for tropical trees: A comparison of three 50-ha plots, *Journal of Ecology* 84 (1996) 549–562.
- [37] J.H. Lawton, D.E. Bignell, B. Bolton, G.F. Bloemers, P. Eggleton, P.M. Hammond, M. Hodda, R.D. Holt, T.B. Larsen, N.A. Mawdsley, N.E. Stork, D.S. Srivastava and A.D. Watt, Biodiversity inventories, indicator taxa and effects of habitat modification in tropical forest, *Nature* 391 (1998) 72–76.
- [38] T.J. Givnish, On the causes of gradients in tropical tree diversity, *Journal of Ecology* 87 (1999) 193–210.
- [39] P. Chesson, Mechanisms of maintenance of species diversity, *Annual Reviews of Ecology and Systematics* 31 (2000) 343–366.
- [40] F.R. Adler and B. Nuernberger, Persistence in patchy irregular landscapes, *Theoretical Population Biology* 45 (1994) 41–75.
- [41] S.W. Pacala, C.D. Canham, J.A.J. Silander, R.K. Kobe and E. Ribbens, Forest models defined by field measurements: Estimation, error analysis and dynamics, *Ecological Monographs* 66 (1996) 1–43.
- [42] D.H. Deutschman, S.A. Levin, C. Devine and L. Buttel, Scaling from trees to forests: Analysis of a complex simulation model, *Science* 277 (1997) 1688.
- [43] J. Chave, Study of structural, successional and spatial patterns in tropical rain forests using TROLL, a spatially explicit forest model, *Ecological Modelling* 124 (1999) 233–254.
- [44] D.L. DeAngelis and L.J. Gross (eds.), *Individual-Based Models and Approaches in Ecology* (Chapman and Hall, New York, 1998).
- [45] R. Durrett and S.A. Levin, Spatial models for species-area curves, *Journal of Theoretical Biology* 179 (1996) 119–127.
- [46] S.P. Hubbell, *The Unified Theory of Biodiversity and Biogeography*, Monographs in Population Biology 32 (Princeton University Press, 2001).

- [47] J. Chave, H.C. Muller-Landau and S. Levin, Comparing classical community models: Theoretical consequences for patterns of diversity, *American Naturalist*, in press.
- [48] P. Köhler, J. Chave, B. Riéra and A. Huth, Long-term response of tropical rain forests to the effects of fragmentation, *Conservation Biology*, submitted.
- [49] D.J.D. Earn, S.A. Levin and P. Rohani, Coherence and conservation, *Science* 17 (2000) 1360–1364.
- [50] E.G. Leigh, Jr., S.J. Wright, E.A. Herre and F.E. Putz, The decline of diversity on newly isolated tropical islands: A test of a null hypothesis and some implications, *Evolutionary Ecology* 7 (1993) 76–102.
- [51] P. Beier and R.F. Noss, Do habitat corridors provide connectivity? *Conservation Biology* 12 (1998) 1241–1252.
- [52] K. Riitters, J. Wickham, R. O'Neill, B. Jones and E. Smith, Global-scale patterns of forest fragmentation, *Conservation Ecology* 4 (2000) 3.
- [53] J.G. Liu and P.S. Ashton, FORMOSAIC: An individual-based spatially explicit model for simulating forest dynamics in landscape mosaics, *Ecological Modelling* 106 (1998) 177–200.
- [54] R.D. Holt, S.W. Pacala, T.W. Smith and J. Liu, Linking contemporary vegetation models with spatially explicit animal population models, *Ecological Applications* 5 (1995) 20–27.