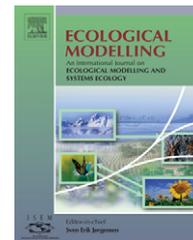




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Changes of species diversity in a simulated fragmented neutral landscape

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ABSTRACT

To predict how ecological communities respond to large-scale patterns of fragmentation, both local and global processes need to be combined into an integrated modelling approach. Using neotropical rain forests as an illustration, we constructed a large metacommunity (200 km × 200 km) where all the trees ≥ 10 cm dbh are modelled, assuming panmixis within local communities (each 10 km × 10 km in size), and limited dispersal across communities. Under the assumption of neutrality, we simulated an equilibrium configuration, that we subsequently submitted to several scenarios of environmental fragmentation. Fragmentation leads to a significant reduction of species diversity in edge communities. After the disturbance, the system returns to equilibrium rapidly if the disturbance is not too widespread, due to dispersal from neighboring areas. However, post-disturbance levels of local diversity remain much lower than pre-disturbance ones, at least within ecological times. These results illustrate the claim that neutral landscape models exhibit a partly predictable ecological-time dynamics, mostly driven by the ability of the metacommunity to buffer accidents in local communities. Such a multi-scale model should be considered as a null scenario in testing more complex effects related to habitat fragmentation, such as genetic bottlenecks, or loss of keystone species.

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1. Introduction

The science of complex systems has emerged from the need of understanding the emergent features of hierarchical structures made of strongly coupled modules (Simon, 1962), such as human societies or biological organisms, for which mathematical models originally developed by engineers are inappropriate. At stake in the emergence of this new science is our ability to make reliable predictions on the fate of real systems, and assess the risks associated with their temporal evolution. Ecological systems provide a great example of complex systems for which attempts have been made to develop predictive models. The rapid degradation of natural biota through land

conversion or harvesting is having a rapid widespread impact on the ability of biological species to maintain stable populations. An oft-cited example of endangered population is wild salmon. It has become critically endangered in the Northwest United States due to a conjunction of river dam development, hatchery misuse, habitat degradation, and over-harvesting, all of which are related to diverse yet convergent mechanisms yielding an increase in economic welfare (Mann and Plummer, 2000). Like salmon, many species are facing critical levels of population decrease, recent tropical examples such as Central American frogs, or Bornean orang-utans being a reminder of this harsh reality (Blaustein and Dobson, 2006; Goossens et al., 2006). Risk assessment programs are being implemented

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to address these issues, and hopefully lead to development policies better integrated with environmental concerns.

Like in the salmon case, species can seldom be considered as being disconnected from their biotic environment, and this is a major challenge in the development of predictive risk assessment models. For instance, the local extinction of a top predator might lead to unexpected and dramatic outcomes in terms of the survival of directly or indirectly related species (Paine, 1966; Durrett and Levin, 1998; Kareiva and Levin, 2003). Because it is impossible to parameterize ecological models that would maximize generality, realism, and precision simultaneously (Levins, 1966), one temptation is to take an approach that focuses on the interaction of single species with its environment, thus moving away from the biological processes that operate at the community level (Lawton, 1999). In a recent essay on this theme, however, Simberloff (2004) re-emphasized the importance of community thinking in ecology, and stressed the dangers of disregarding interspecific interactions on the sole reason that the predicting power of such an approach is contingent on the idiosyncrasies of the system under study. He advocates the need of ambitious research programs that combine theoretical development and careful empirical testing of the theory. From the above discussion, it becomes apparent that two sources of uncertainties are intimately associated to ecological modelling exercises: the first, to the model construction, and the second, to the ability to make reliable predictions within the frame of work of the selected model.

In this paper, we take on this fundamental issue, taking tropical tree communities as an illustration. Tropical forests make a large contribution to the Earth's biodiversity, and they also largely contribute to carbon cycling (Malhi and Grace, 2000), an essential ecosystem service (Kremen, 2005). Besides, they are a key resource for many human populations. Because of recent land-use changes related to economic development (Achard et al., 2002), and of intensive logging (Asner et al., 2005), this biome has undergone dramatic changes over the past decades, and it might be on the verge of a rapid collapse. Here we assess one of the potential consequences of these rapid changes on tropical forest plant biodiversity at the metacommunity level (for a definition, see below, and in Holyoak et al., 2005). Many previous studies have ignored the larger scale, placing a strong looking for mechanisms involved in environmental degradation at the local community scale. However, both biogeography and evolutionary theory have taught us that the most important processes of species coexistence act at the regional scale, not solely at the local scale (Ricklefs, 1987). The first-order effect of fragmentation on tropical trees is the decrease in size of the suitable area, and the reduction in abundance in most of the populations inhabiting the disturbed environment. An additional essential effect is the inability for the species restricted to limited patches to re-colonize a previously degraded habitat, owing to their limited dispersal ability. Though tropical forests have long been heralded as ranking among the most complex ecosystems, we here advocate for a rather simple, yet insightful, modelling perspective. The model we develop and discuss includes several key features of complex ecological communities: multi-scale temporal variability and spatial structure (Levin, 1992). As can be argued no matter how detailed a model be, many other

mechanisms might act to accelerate the erosion of biodiversity following the rapid shrinking of a biome (genetic bottlenecks, Allee effects). Yet, we shall not incorporate them in our model, and we will develop on this in the Section 3.1.

The specific question we are here asking is whether we can predict the long-term impact on species diversity in a large biome under scenarios of human-induced environmental change. We shall assume that this change mostly results in a decrease in the area for the tropical forest biome. Our main question was: can one predict the outcome of the fragmentation process on levels of biodiversity, due to demographic processes (reduced migration, decrease in population sizes), and irrespective of the micro-environmental alterations predicted to occur in such a condition (see e.g. Laurance et al., 2004)?

2. The model

2.1. Dynamics in a local community

The model we develop is a spatially explicit modification of a spatial neutral model, already explored by Hubbell (2001, chapter 7). The metacommunity (Holyoak et al., 2005) under study is partitioned into a grid of D local communities interacting through dispersal (Fig. 1). The total number of individuals in the metacommunity is J_M . At any given time, each local community hosts a number J of individuals, such that $J_M = D \times J$. Our forward-time modelling of the metacommunity dynamics allows us some further flexibility compared with commonly made assumptions in similar spatially structured models (Crow and Kimura, 1970; Maruyama, 1972). We can vary the local community size both in space and in time, thus

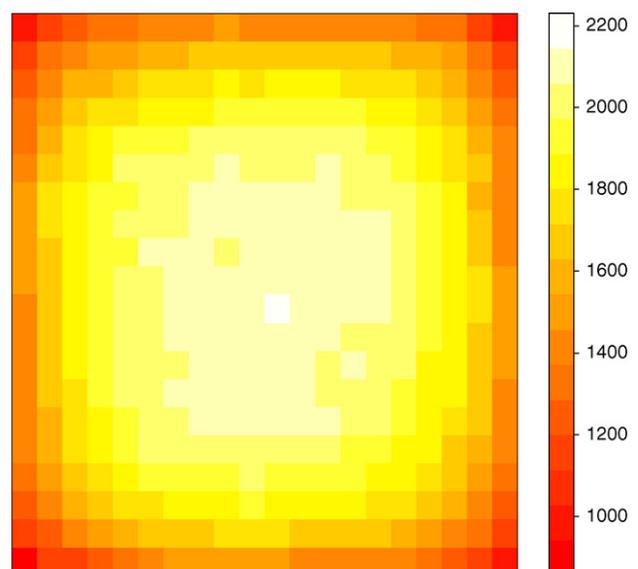


Fig. 1 – Number of species in the $D = 20 \times 20$ simulated local communities. Each local community has $J = 5,000,000$ individual trees ≥ 10 cm dbh, that is, it covers about 100 km^2 . Because of edge effects, communities at the boundary of the domain harbor a lower species richness than that around the center of the metacommunity.

modelling processes of wide-scale community collapse followed by recovery and realistic spatial patterns of niche filling. Because we are here interested in the issue of the uncertainty associated with the short-term prediction of species diversity, we shall not explore all of these variants.

In each local community, the species abundance distribution is summarized by $N_k, k \in \{1, \dots, S\}$, the number of individuals of species k in the community, such that $\sum_k N_k = J$, and where S is the total possible number of species in the metacommunity (possibly, $N_k = 0$). The local community dynamics can be modelled by a Fisher–Wright dynamics with no generational overlap (Fisher, 1930; Wright, 1931), or by a Moran dynamics (Moran, 1962) with generational overlap. In the first case, individuals at time t are all new individuals descending from those present at time $t - 1$. In the second case, only a fraction of the individuals is replaced. Both processes are simulated using a multinomial deviate generation (MDG) procedure. In the MDG, we set $p_k(t) = N_k(t)/J$, the expected relative abundances of species k at time t . For the Fisher–Wright model, we select S multinomial deviates $N_k(t + 1)$, generated from parameters $\{p_1(t), \dots, p_S(t)\}$, and such that these numbers verify $\langle N_k(t + 1) \rangle = p_k$ and $\sum_k N_k(t + 1) = J$. The configuration is the new species abundance distribution at time $t + 1$. For the Moran dynamics, only a fraction τ of the individuals is replaced each time step: $\tau \times J$ individuals are killed irrespective of the species they belong to, and the empty niches are immediately filled by the offspring of individuals of the local community or of neighboring communities. This second step makes again use of the MDG procedure.

New species appear in the local community through various processes. For instance they may appear by point-wise speciation, where an individual in the metacommunity is suddenly replaced by an altogether new species. In plants, this may correspond to the appearance of a polyploid type (Stebbins, 1950) possibly combined by more complex patterns of genome duplication (Soltis, 2005). The second process is that of allopatric speciation, whereby two populations diverge after being isolated by distance. This second process has long been thought of as being crucial in evolution (Mayr, 1963). Here we model the appearance of new species in the community by a method that can be interpreted either as sympatric speciation followed by some degree of hybridization, or as the divergence of a peripheral isolate. We select a fraction ν of the species at random and split them into two species, assuming that on average p of the initial species remains unaltered and that the remaining $1 - p$ becomes a new species (the actual abundance of the new species is drawn from a binomial distribution, with parameter p drawn uniformly in $[0, 1]$).

2.2. Dynamics in a spatially subdivided metacommunity

The spatial process is modelled through a stepping-stone dynamics, whereby only neighboring local communities interact through dispersal. If $N_{i,j,k}$ is the abundance of species k in the local community $[i, j]$, then the average abundance in the neighborhood for this species is

$$\langle N_{i,j,k} \rangle = \frac{N_{i,j+1,k} + N_{i,j-1,k} + N_{i+1,j,k} + N_{i-1,j,k}}{4}$$

We chose to model the dispersal process by $N'_{i,j,k} = (1 - m)N_{i,j,k} + m\langle N_{i,j,k} \rangle$, where the parameter m represents the migration rate from the surrounding local communities, that is, the probability that an individual present in the community is an immigrant. This formulation is a discrete analog of the continuous diffusion process described, e.g. by Skellam (1951). It would be easy to generalize this formalism by introducing a spatially dependent migration matrix $m_{i,j}$ (Bodmer and Cavalli-Sforza, 1968), representing the number of individuals born in the i -th colony from parents in the j -th colony.

Because of dispersal limitation, a spatial structuring of the species populations is expected to take place in the metacommunity. The theoretical properties of a spatially structured model of metacommunities are not all well-known. In the limit where J is very large, and migration connects all local communities, a continuous description can be provided that traces back to Fisher's (1930) and Wright's (1931) distribution for gene frequencies. In the case of Wright's island model (Wright, 1943), one infinite-size local community is connected with a regional species pool through immigration m , and the coexistence of wild types is therefore the by-product of immigration and of local extinction. Wakeley (2003) studied this model theoretically for J finite, but for a large number of local communities D , and assuming that new types arise punctually in the metacommunity at a rate ν (mutation rate in his terminology). Also, he assumed that m was an immigration rate from any possible local community, rather than from the immediate neighbors as we here assume. In this limit, he found that spatial subdivision slows down the process of species divergence, though most of the spatial patterns remain unaltered.

2.3. Simulating an equilibrium state

We simulated a tree community in a tropical forest landscape. Local communities were assumed to be square cells of size $10 \text{ km} \times 10 \text{ km}$. In most Amazonian forests, one finds on the order of 500 trees above 10 cm dbh per hectare (ter Steege et al., 2003). Scaling up to the cell area, we predict that J is equal to 5,000,000. To explore patterns of temporal variation under several scenarios of fragmentation, we focused on an area of $200 \text{ km} \times 200 \text{ km}$ (400 local communities), or about 0.5% of the total forested area in Latin America (Achard et al., 2002). This represents a total of 2×10^9 individuals. We estimated that the number of species in a simulated neotropical tree metacommunity of this size was up to $S = 8000$ species. We ran simulations starting from uniform initial conditions such that all the species in all the sites had the same abundance. Assuming a death rate of about 1–2% per year for adult trees, one generation is estimated to be about 50 years. A first run of 200,000 Fisher–Wright time steps was performed to produce a realistic landscape, where extinction and speciation are balancing at the metacommunity scale. In the corresponding 10 Myr, tropical forests have undergone numerous events of speciation and extinction (Davies et al., 2005), so we expect that our simulation reflect appropriately a realistic process of metacommunity buildup. We followed this stage by 30,000 Moran steps (30,000 years). The param-

Table 1 – Value and interpretation of the parameters used in the simulations

Parameter	Interpretation	Values
Metacommunity parameters		
J	Local community size	5,000,000
A	Local community area (km ²)	100
D	Number of local communities	400
J_M	Metacommunity size	$J \times D$
S	Total number of species	2000
ν	Speciation rate (generation ⁻¹ site ⁻¹)	0.0002
m	Migration rate (generation ⁻¹)	0.0002
Community buildup phase		
r	Rate of regrowth (generation ⁻¹)	0.01
τ	Generation duration (years)	50
T	Number of time steps (generations or years) ^a	–

^a Depending on whether the Fisher–Wright or the Moran dynamics are chosen.

eter values used in the simulations are summarized in Table 1.

2.4. Scenarios of fragmentation

Starting from the simulated initial condition, we performed several scenarios of forest fragmentation.

First, we assumed that the area was disjunct by the construction of a paved highway (see e.g. Laurance et al., 2001). The fragmentation was followed by a simulated sequence of 1000 years, during which the impact on diversity was explored. Then, for another 1000 years, the species could invade the area, keeping the rate of increase of local populations at 1%/year, that is, ca. 50,000 individuals per year, randomly sampled from the neighboring community.

We also simulated a scenario of clustered fragmentation of the area, with various fragmentation intensities. We let the system evolve during 200 years after fragmentation, assuming various fragmentation intensities f , ranging from 0.5 to 0.99. We then recorded the remaining fraction of species in the metacommunity.

The simulated data were post-processed using the R statistical software (<http://www.r-project.org/>).

3. Results

The simulated landscape showed ecological patterns of species abundance consistent with those commonly observed in real tropical forests. With our choice of parameters, and the simulated history, the species diversity of local communities varied between 900 and 2200, with a marked mid-domain effect (Fig. 1, see e.g. Colwell et al., 2004), and about 5800 species in the metacommunity. The local rank abundance distributions were also consistent with most observations (Fig. 2, Whittaker, 1972; Hubbell, 2001). Species distributions were generally markedly clumped, both for abundant and for rare species (Fig. 3).

We used this case study to explore various patterns of fragmentation. In a scenario of fragmentation by a large highway preventing dispersal, we observed that the area surrounding the highway, and the most species rich zone had a significant depletion of the local diversity of up to 250 species. This depletion could not be accounted for by stochastic processes only (Fig. 4). This species reduction was detectable shortly after fragmentation, but this effect built up slowly thereafter.

After the fragmentation stage, we allowed the plants to invade the area for another 1000 years. Given the very large pool in the surrounding local communities ($J = 5,000,000$), diversity replenishment was rapid: within 50 years, the local communities were saturated. However, this process resulted in a significantly poorer local diversity than before species fragmentation: the fragmented flora harbored 900 species versus about 1300 before fragmentation (Fig. 5).

We found an important effect of fragmentation on the metacommunity diversity only at high fractions of disturbance. For $f = 0.95$, a figure comparable to that observed in the Atlantic forests of Brazil (Mori, 1989), we found that 77% of the species were still present in the metacommunity after 200 years (Fig. 6). Hence, the role of migration to maintain local diversity was greatly reduced.

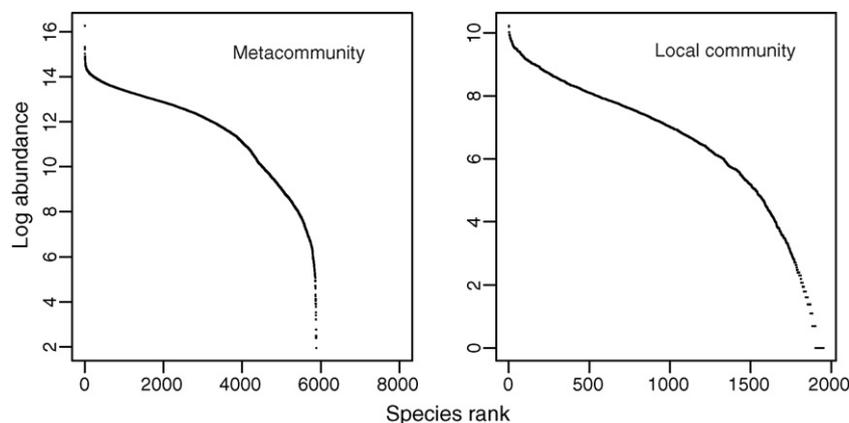


Fig. 2 – Rank abundance distributions of the whole metacommunity (left panel) and of one local community (right panel). The most abundant species in the metacommunity had about 10^7 individuals.

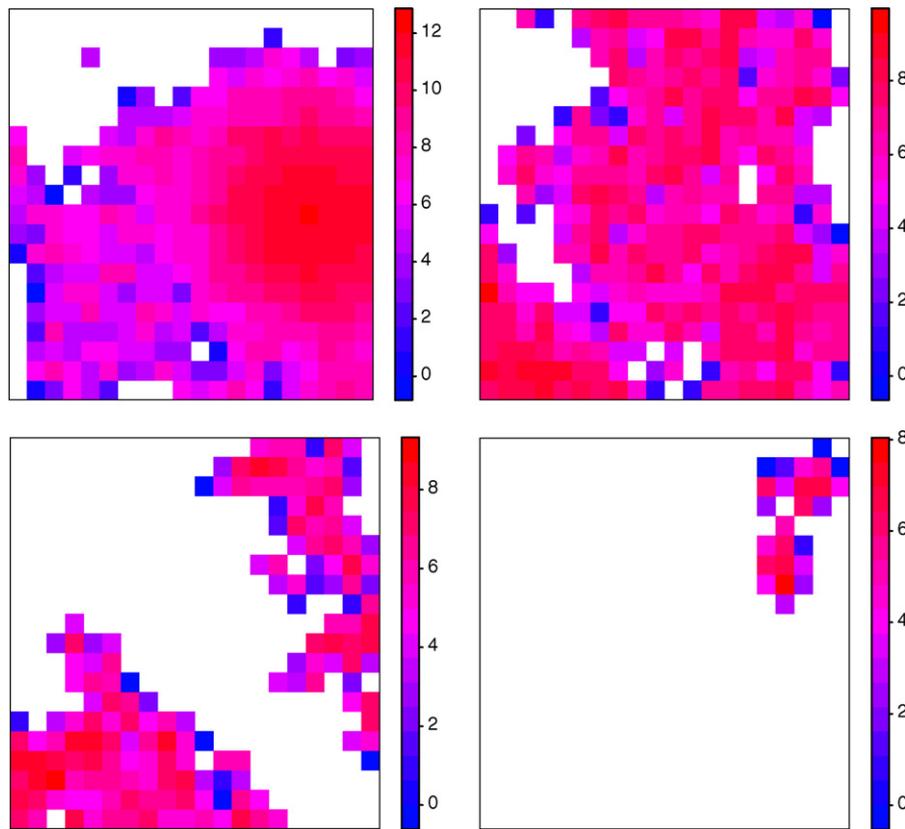


Fig. 3 – Spatial distribution of four species. The color key corresponds to the log-transformed abundance of the local species in each of the 400 simulated local communities. Top left panel: distribution of the most abundant species in the metacommunity; top right and bottom left panels: species of intermediate abundance; bottom right panel: regionally rare species.

3.1. Discussion

In this study we have described how a large-scale model of metacommunity dynamics could be developed. This model reproduces the local population dynamics at both evolutionary and ecological-time scales, migration processes, species apparition through processes of speciation, and spatial pat-

terns. Our scenarios mimicked situations where a forest is entirely clear-cut, as well as scenarios of habitat disturbance, such as in selectively logged tropical forests. Our main findings are that: (1) in a fragmented neutral landscape, species diversity decreases globally, not only within the disturbed communities; (2) species diversity decreases as a non-linear function of environmental fragmentation and (3) the return to

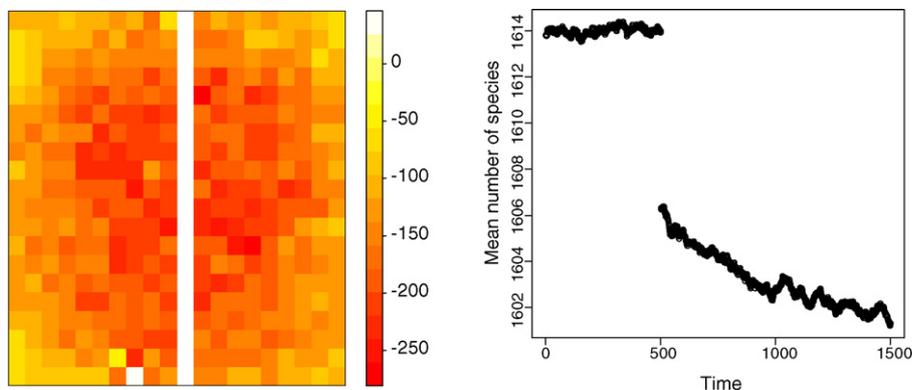


Fig. 4 – Potential dispersal limitation and edge effects due to the establishment of a paved highway. Left panel: difference between local species richness immediately before and 1000 time steps after fragmentation in each local community. The largest species losses are observed in the central zone, near the fragmented area. Right panel: mean local diversity over time, 500 time steps before and 1000 time steps after fragmentation. In this simulation, 1 time step corresponds to 1 year.

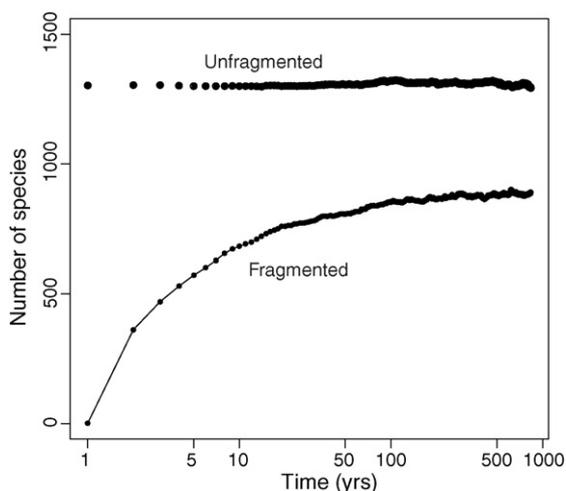


Fig. 5 – Increase of local species richness in the fragmented area of Fig. 4. Diversity increases steeply for the first 50 years, then much more slowly. After 1000 time steps, local diversity is about 70% of its pre-fragmentation level (upper line).

dynamic equilibrium following a disturbance does not necessarily mean a return to pre-disturbance levels of local diversity. These three patterns were intuitively expected, but we here shed a different light on them by evidencing that they are consistent with a very simple neutral dynamics.

Several works have addressed the issue of the impact of tropical forest fragmentation on community dynamics. Leigh et al. (1993) studied six islands created in 1913 by the formation of Gatun Lake, Central Panama. They found a decrease in local diversity as a result of this fragmentation. Over a larger scale, more relevant to the present study, Laurance et al. (2004)

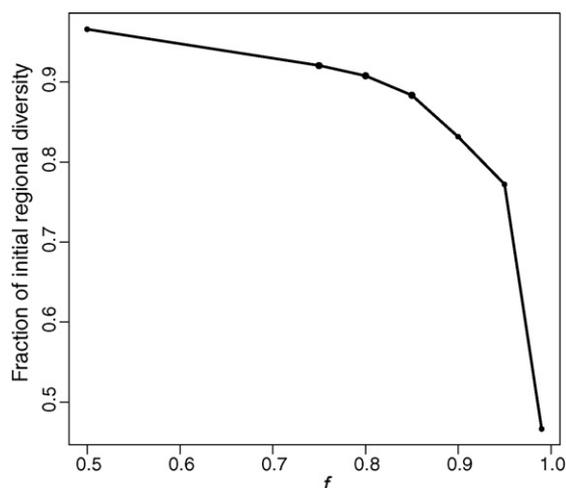


Fig. 6 – Regional diversity as a function of the fraction of fragmented landscape, f , 200 years after fragmentation. A random pattern of fragmentation was assumed, that is, a fraction f of the local communities was completely emptied at the beginning of the simulation. Regional species diversity was represented as a fraction of the undisturbed regional diversity (here, 5883 species).

studied changes in abundance for tree genera over a period of 20 years in a fragmented rain forest near Manaus, Brazil. They failed to show a significant decrease in local diversity at this scale, but evidenced directional trends in genus-level abundances. This apparent maintenance of large diversity levels does not contradict our own findings, as this previous study was short-term trends only, and was based on small samples of the local communities, thus under-representing the rarest species. Our conclusions 1 and 2, that fragmentation has a widespread impact of the metacommunity even for seemingly mild disturbances such as our highway scenario, therefore suggest that decline in diversity should be a longer-term consequence of fragmentation, and might become significant in empirical studies only after several decades. In addition, while differential species-specific response are likely to bring important ecological as well as conservational insight, we stress that our approach enables a simple assessment of the impact of fragmentation on total species diversity, not only on the extinction risk for a handful of species. There is no question that essential ecological processes are acting on tropical trees communities and may be altering our conclusions. For instance, the impact of climatic change or other large-scale environmental effects (e.g. N deposition, CO₂ increase) might lead to rapid species shifts in the tropical vegetation (Malhi and Grace, 2000; Phillips et al., 2002; Laurance et al., 2004), with directional changes in the abundance of some species groups. We could have included such non-neutral changes in our simulations, but this would have led to many more assumptions and details. We hope that the present study will stimulate further research bringing together metacommunity ecology and global change modelling.

Recently, Holyoak et al. (2005, chapter 1) have provided a useful overview of our current understanding of ecological processes at the metacommunity scale. They have emphasized the lack of conceptual tools for scaling up the ecological issues beyond the scale at which they are commonly studied empirically. In their excellent review of competing metacommunity theories, Chase et al. (2005) suggest the neutral framework as an interesting option for explaining observed metacommunity patterns. A number of predictions have already been tested either empirically or theoretically in the neutral framework. One of the main purposes of our present study was to explore another such pattern, namely how fast neutral metacommunities return to an equilibrium after a local disturbance (see Table 14.1 in Chase et al., 2005). The answer we provide (conclusion 2) is consistent with the predictions of Chase et al. (2005): local communities return quickly to an equilibrium. However, because we simulated a spatially explicit system we discovered that in our system, the post-disturbance level of species diversity differed from the pre-disturbance one, corresponding to slightly over two-third over the initial species diversity (Fig. 5). Theoretical results suggest that the initial species diversity should be recovered at some point, but not over an ecological-time scale. Hence, we were able to address not only the effects of local disturbance, but also the effects of dispersal reduction due to spatial fragmentation.

The results above are based on the assumption that all individuals have the same prospects of recruitment and death, irrespective of their species. This assumption of neutrality is

controversial in ecology and it has generated a considerable amount of debate in recent years (see e.g. Bell, 2000; Hubbell, 2001; Chave, 2004; McPeck and Gomulkiewicz, 2005). One of our motivations for using this theoretical framework is that it greatly facilitates the numerical implementation of the model, and that exact mathematical results can be derived. We were able to simulate the long-term dynamics of a very large system, with about 10^9 individuals in 100 local communities and simulated for over 10,000 generations. It remains difficult to reach such large scales in non-neutral individual-based models (DeAngelis and Mooij, 2005). For instance, Chave (1999) ran a forest model simulator on a massively parallel computer to simulate the dynamics of ca. 10^7 plants during 1000 time steps, that is two orders of magnitude less than the present study and 10 times shorter time scales. Similarly, Köhler et al. (2003) simulated patterns of fragmentation in a rain forest of French Guiana using a fully parameterized physiology-based forest simulator in an area of 1 km^2 , also two orders less than the present simulation. The neutral assumption enabled us to keep track of local species abundances instead of individual features, yet preserving many of the crucial processes, such as local demography, migration, speciation, and variable community size. Despite the simplicity of our assumptions, the above results are not obvious, being a result of the interplay between several processes such as drift, speciation, and limited dispersal across scales.

Some of our results are compatible with theoretical predictions of population biology (Wright, 1943; Crow and Kimura, 1970). Under the assumption of neutrality, or of weak selection, in subdivided populations, one can for instance derive expressions for the spatial autocorrelation of diversity (Maruyama, 1972), for the time to extinction (Barton, 1993), or for the equilibrium distribution of allele frequencies (Wakeley, 2003). Most of our simulated results could have been obtained using a backward-in-time genealogical approach, where the species identities of individuals are tracked by constructing a genealogy constrained by modes of speciation and of migration (Chave et al., 2002). The forward-in-time approach has advantages, however, in that it is more intuitive to most ecologists, and enables a simple implementation of fragmentation processes. Moreover, the MDG procedure implemented here reduces considerably the computational burden.

One of the most interesting results of our study is that the dynamics was largely predictable over ecological timescales. We emphasize this point because it is often assumed that a neutral model should display essentially stochastic, thus unpredictable, patterns. Because the metacommunity was established over long time scales, a hierarchy of species abundances has slowly settled in the metacommunity, and it is not expected to change by large amounts over ecological-time scales. Since we are dealing with huge population sizes, on the order of 10^6 individuals per species, it should come to no surprise that the neutral species dynamics is slow for abundant species, and fluctuations are relatively small. This illustrates the fact that our knowledge of biodiversity processes is above all limited by our ability to sample exhaustively large biomes, and explore ecological properties at the metacommunity level (McPeck and Gomulkiewicz, 2005). We still do not have the appropriate tools for approaching

the most pressing issues about biodiversity at the regional scale.

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