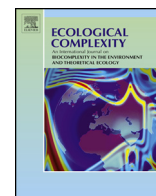




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Original Research Article

# Extinction debt and the role of static and dynamical fragmentation on biodiversity



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## ABSTRACT

The mass-extinction events caused by human-driven habitat loss are a current concern in conservation science. However, the observed number of extinctions is considerably smaller than predicted. The overestimation of extinction rates comes from the time-delay which depends on the species sensitivity to habitat changes. The standard method of predicting the effect of habitat loss on biodiversity is to use the species–area relationship and progressively following it backwards to smaller areas. The difference between the actual number of species and the one provided by the backwards species–area relationship is dubbed extinction debt. Previous studies in general adopt a static view for the spatial distribution of species. Nonetheless, a precise understanding of the problem urges us to adopt a dynamic framework to this issue since the time between disturbances of the landscape plays an active role in influencing the strength of the extinction debt. In this context, here we address two distinct approaches for this question: a static and a dynamic view of fragmentation. In the former we quantify the extinction debt in a quenched spatial distribution of species, whereas in the latter the community is let to evolve between disturbance events of the landscape. Here we show that the size of the extinction debt depends on the pattern of the fragmentation. It is found that random distributions of destroyed habitats provide larger extinction debts than those obtained for contiguous areas of fragmentation. Furthermore, in the dynamic approach it is observed that dispersal can lead to unexpected outcomes such as lower biodiversity levels than ones inferred from the backwards species–area relationship.

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## 1. Introduction

Empirical evidences demonstrate that recent extinction rates are 100–1000 times higher than background rates (He and Hubbell, 2011; Pimm et al., 1995). Habitat loss and fragmentation are considered as the major mechanisms driving the shrinking of biological diversity in earth (Holt et al., 1995; Wilcove et al., 1998; Balmford and Bond, 2005; Damschen et al., 2006), and hence species extinctions are mostly resulted from the competition for resources and space with humans. The understanding of the effect of habitat fragmentation on ecosystems is crucial in finding alternative solutions to minimize its impact and making-policy recommendations (Mendenhall et al., 2014). In this context, the great majority of research either focused on effects of fragmentation on metapopulations (Hanski and Ovaskainen, 2000; Levins, 1969) or on the dynamic patch-occupancy (Caswell and Cohen, 1991; Hill and Caswell, 1999), and aimed to address the balance

between colonization and local extinction. A more thorough study about metapopulation persistence that combines patch dynamics and dynamic landscapes has also been presented (Keymer et al., 2000). An important finding is that in metapopulations, connectivity plays an influential role in the way that ecosystems respond to habitat loss and change (Hanski and Ovaskainen, 2000; Hylander and Ehrlén, 2013).

The species–area relationship (SAR) is a central concept in ecology (Lomolino, 2000). The species–area relationship informs us the rate at which species richness increases along a gradient of ecosystems of increasing size. In this way, the SAR is also used as an indirect manner to assess the impact of habitat loss or habitat change on biodiversity by reversing it, bringing it backwards to smaller areas. Nonetheless, the method usually overestimates the biodiversity loss. The discrepancy between prediction and observation, referred to as extinction debt, may be explained by the fact that local and global extinctions are delayed (Hylander and Ehrlén, 2013). Thus extinction debt can also be considered to be an estimator of the number of endangered species in the community. By taking a static view for the community, this quantity is always positive. After a long time has elapsed from the disturbance it is

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expected that the number of species will relax to the number predicted by the SAR.

The current work aims to survey how the process by which habitat loss occurs can affect species richness in a neutral community. In the most straightforward model of fragmentation habitat loss is achieved by randomly removing suitable habitats, corresponding to a null model of fragmentation. Although habitat deterioration is seldom a random trial. Landscape patterns in disturbed environments are better described by fractal structures which are resulted from the complex interaction between natural processes and human-management (Krummel et al., 2012). The size–shape relationships of the altered landscape can play influential role on important ecological mechanisms such as dispersal, extinction and speciation (Birand et al., 2012). Here we control the way fragmentation occurs by tuning the level of spatial autocorrelation of the landscape. The procedure generates very distinct landscapes structures as the amount of unsuitable habitats is increased. In the model, fragmentation follows a fractal pattern. The configuration and distribution of suitable/unsuitable habitats are controlled by a fractional Brownian motion, which produces spatially correlated landscapes. Fractal landscapes have been used to study fragmentation effects on the persistence of single species which is under the balance between colonization and local extinction (Hill and Caswell, 1999). It has been shown that species responses to habitat change and fragmentation which rely on the properties of the species themselves (Hill and Caswell, 1999; Hanski and Ovaskainen, 2000), but also on the spatial arrangement of landscape disturbances (Hill and Caswell, 1999). Nevertheless, an investigation about how landscape disturbance and its spatial arrangement affect the strength of extinction debt is still missing. The analysis here is developed within two distinct frameworks. In the former we adopt a static approach to inquire how habitat loss and its spatial arrangement modify the magnitude of extinction debt. In this approach, a community is put to evolve in a homogeneous landscape until equilibrium and then fragmentation ensues. The community is no longer allowed to evolve. This is the standard method used to infer the impact of fragmentation on extinction rates (He and Hubbell, 2011). However, a full understanding of the impact of habitat destruction requires a dynamic approach whereby the community is not quenched but rather is subjected to ecological processes such as dispersal, speciation and extinction between the events landscape disturbances. In both situations the role of long-range dispersal is addressed. We consider a neutral community, and so species are seen as functionally equivalent without niches differences, but with slow drift to extinction offset by speciation (Hubbell, 2001). The dynamics is equivalent to the voter model of Durrett and Levin (Holley and Liggett, 1975; Durrett and Levin, 1996).

The paper is organized as follows. In the next section we describe the model and the methodology employed in the work. In the following we present our simulation results for both static and dynamic frameworks of fragmentation. We also show how dispersal can affect the magnitude of extinction debt. And finally in the last section we draw our conclusions.

## 2. Materials and methods

### 2.1. The model

We consider a community in which individuals are initially distributed over a homogeneous two-dimensional lattice of sides of length  $L$ . Therefore the network comprises  $N = L \times L$  habitats. Initially all habitats are considered suitable and because only one single individual can occupy a suitable habitat the initial community size is also equal to  $N$ .

In the beginning the community is isogenic, i.e. all individuals belong to the same species. Subsequently, the community evolves according to the neutral dynamics of the voter model with mutation (Durrett and Levin, 1996). A basic assumption of the neutral dynamics is the selective equivalence of species, a premise of the unified neutral theory of biodiversity and biogeography (Hubbell, 2001). At each time step a randomly chosen individual dies and gives rise to a new species (speciation event) with probability  $\nu$ , or its position is filled by a species randomly picked out from its neighborhood with probability  $1 - \nu$ . In the original version the neighborhood comprises the four immediate neighbors of the focal cell (von Neumann neighborhood). Note that as soon as an individual is removed, its position is immediately filled up. Therefore, each time step corresponds to a death event, and the parameter  $\nu$  is the speciation rate in units of the death rate. The von Neumann neighborhood long-range dispersal is also simulated. In the latter case whenever an individual dies, with probability  $1 - \nu$ , it is replaced by any individual inside a square kernel of size  $N_D = K \times K$ , with  $K$  denoting the linear size of the dispersal kernel.

The community is let to evolve until an equilibrium regime is reached. In the equilibrium the species richness fluctuates around a given value. The time to equilibrium can be considerably large and is proportional to  $1/\nu$ . After the equilibrium regime is reached the species–area relationship is obtained. The next stage of our modeling is to execute the fragmentation process by removing suitable habitats, i.e. suitable habitats are brought over into unsuitable ones (habitat loss). This procedure effectively reduces the available area to the community and hence one can obtain the number of species as a function of effective area as habitat loss advances. The most straightforward manner to simulate landscape perturbation is randomly selecting and converting suitable habitats into unsuitable ones. Following this procedure, as the fraction of suitable habitats  $p$  drops below the site percolation threshold  $p_c \simeq 0.5927$  a cluster of suitable cells spanning over the lattice will cease to exist and the landscape structure comprises a high number of small and unconnected clusters. The critical concentration  $p_c$  is referred to as the percolation threshold (Stauffer and Aharony, 1992; Campos et al., 1997).

Although it is pretty clear that the extent of the environmental perturbation strongly influences the number of extinctions (Kuussaari et al., 2009), it is not well established how extinction depends on the spatial autocorrelation of the landscape perturbation. Whether the habitat destruction is either locally restricted (highly clumped) or more random may affect extinction debts in different ways (Tilman et al., 1997). Still, most of the theoretical studies addressing the extent of extinction debt assume random placement of species (He and Hubbell, 2011). Surely, this is an awkward assumption since most species have a small range size and are highly aggregated (Hubbell et al., 2008; Scheuring, 1991; Morse et al., 1985). In our model the spatial distribution of species resulted from neutral dynamics and landscape perturbation is not done in a random fashion. But rather we tune the level of spatial autocorrelation of the fragmented landscape. This process is fulfilled through the use of fractional Brownian motion (fBm) to construct fractal landscapes (Mandelbrot and van Ness, 1968). The fractional Brownian motion produces structures with varying degrees of roughness. The degree of roughness is determined by the Hurst exponent  $H$  which in turn sets the scaling behavior of the fractional Brownian motion (Mandelbrot and van Ness, 1968; Campos et al., 2013). The fBm generalizes the ordinary Brownian motion, which corresponds to  $H = 0.5$ , and the variance of the increments has the special form as

$$\text{var}(X(t_2) - X(t_1)) \propto |t_2 - t_1|^{2H} \quad (1)$$

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