

## Modeling Biodiversity Dynamics in Countryside and Native Habitats

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### Glossary

**Biodiversity dynamics models** Models describing the dynamics of one or more measures or dimensions of biodiversity (e.g., species diversity or population abundances).

**Countryside habitats** A landscape made of native and human-dominated habitats.

**Human-dominated habitat** A habitat that has been significantly altered by humans. Significant habitat alterations include the conversion of natural forest into a pasture or the reclamation of a wetland for agriculture.

**Land use** The set of human activities within a landscape and their impacts on natural processes, such as physical, chemical, and biological cycles. In practice, land use is often classified in major categories such as cropland, pasture, plantation forest, and natural forest.

**Metapopulation model** A model of a population restricted to habitat patches immersed in a matrix used only for dispersal. The population in each habitat patch may go extinct through stochastic processes and recolonized by individuals dispersing from other patches.

**Native habitat** Native habitat is the community of species and the physical environment that occurred in a region before human intervention. In this article, it is equated to

the naturally occurring vegetation in a region. In other contexts, it refers to the particular natural habitat of a given species.

**Phenomenological models** Models that relate observable variables without postulating the underlying (physical, biological, etc.) mechanisms. For example, the species–area relationship is a phenomenological model because it does not explicitly state the mechanisms leading to the relationship between the number of species and area.

**Process-based models** Models explicitly based on mathematical representations of processes or mechanisms, such as animal or seed dispersal. For example, population dynamics models describe the evolution over time of the population abundance by accounting for processes such as birth, death, and dispersal.

**Species–area relationships** The relationship between the size of a given habitat or area sampled across habitats, and the number of species (typically of a specific taxonomic group) found in that area.

**Source-sink population model** A model of a population that occupies multiple habitats in the landscape connected through dispersal. The habitats where population growth is positive are sources and the habitats where growth is negative are sinks.

### Introduction

Despite international efforts and commitments to reduce biodiversity loss, biodiversity continues to decline at high rates compared to those in the background fossil record (Butchart *et al.*, 2010; Barnosky *et al.*, 2011). Land-use change is currently the main driver of biodiversity loss in terrestrial ecosystems and is likely to remain so over the next few decades (Duraiappah *et al.*, 2005; Pereira *et al.*, 2010). It is therefore essential to assess how different patterns of land-use affect biodiversity, in order to compare the biodiversity costs and benefits of different policy and management options.

Much of the recent modeling efforts on biodiversity dynamics of global change have looked at the impacts of climate change (Thuiller *et al.*, 2008; Pereira *et al.*, 2010). However, many of the original projections of global extinction rates were developed from forest loss estimates (Pimm *et al.*, 1995), and there is a renewed interest in models linking biodiversity response to land-use change at different scales (Pereira and Daily, 2006; Wright, 2010; He and Hubbell, 2011). Some of this renewed interest comes from the realization that although the conversion of native habitats to agriculture and other human-dominated habitats is followed by biodiversity loss (Brooks *et al.*, 1999, 2003), countryside habitats can also support important levels of biodiversity, particularly when forest patches or other complex vegetation features remain (Daily *et al.*, 2003;

Ranganathan *et al.*, 2008). Another important issue is that global land-use change dynamics are increasingly complex. While forest loss continues to occur in tropical forests and subtropical woodlands, some regions of the world are seeing an expansion of forest through natural vegetation regeneration or plantations (van Vuuren *et al.*, 2006; UNEP, 2007; FAO, 2010). Therefore, there is a need for models that can capture not only the biodiversity consequences of native forest loss, but also the potential benefits of natural forest expansion or the implications of forest plantations for biodiversity.

Here we review existing models to study the response of biodiversity to land-use change. These models can be grouped in two major categories: phenomenological and process-based (Pereira *et al.*, 2010). Phenomenological models use empirical relationships between habitat characteristics such as area and land-use intensity and species diversity or other biodiversity metrics. The most widely used phenomenological model is the species–area relationship (SAR), and it illustrates the approach of this type of model. There is a well-known relationship between the size of an area and the number of species in that area (Rosenzweig, 1995). The assumption is that the SAR can be applied to project the number of extinctions as a consequence of loss of area of native habitat, even if we do not explicitly model the processes that cause the relationship between the size of an area and its number of species. In contrast, process-based models try to capture the processes that

underlie the relationship between land use and biodiversity. For example source-sink models (Doak, 1995; Pereira *et al.*, 2004) describe the population dynamics of species in habitats of good quality and habitats of poor quality and the movement of individuals between those habitats. Land-use change modifies the proportion and the spatial configuration of the habitats in the landscape. Therefore, in source-sink models there is an explicit link between the land-use change processes and species population dynamics.

## Phenomenological Models

### Native Habitats: Species–Area Relationship

It has been long known by ecologists that the number of species in a given area increases with the size of the area (Arrhenius, 1921). Several expressions have been proposed to describe the relationship between number of species,  $S$ , and the size of an area,  $A$ , with the most common one being the power law (Dengler, 2009):

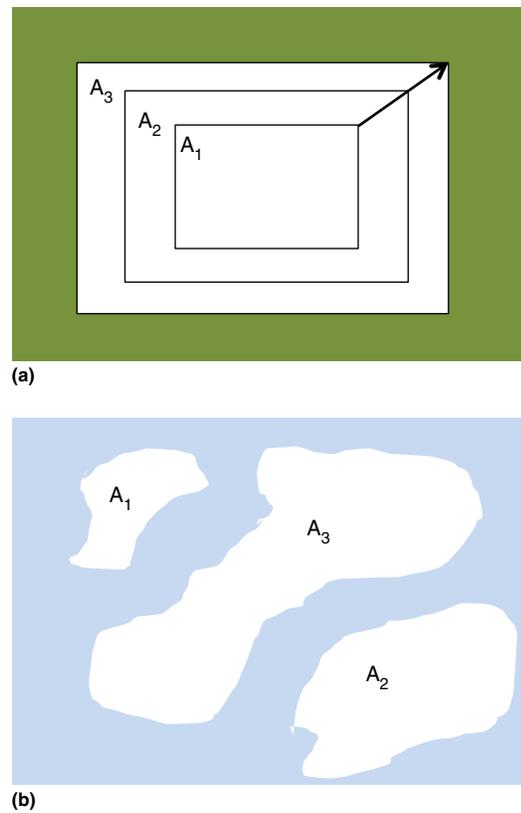
$$S(A) = cA^z \quad [1]$$

where  $z$  depends on the sampling regime and scale and  $c$  depends on the taxonomic group and region (Rosenzweig, 1995). Therefore, if there is a habitat loss of area  $a$  from a total area  $A$ , the proportion of species going extinct can be estimated as

$$\frac{S(A) - S(A - a)}{S(A)} = 1 - \left(1 - \frac{a}{A}\right)^z \quad [2]$$

The problem is that, in general, (1) is estimated from patterns that were generated by very different processes from the habitat loss patterns that (2) aims at describing. There are two general types of sampling for the SAR (Drakare *et al.*, 2006; Dengler, 2009): nested sampling and isolate sampling. In nested sampling, progressively larger areas of a continuous ecosystem are sampled, usually nested within each other (Figure 1(a)). The SARs generated by this type of sampling are also known as continental SARs (Rosenzweig, 1995), as in most cases they come from studies on continents. In isolate sampling (Figure 1(b)), habitat isolates with different area sizes are sampled. Initially, most of the SARs using isolate sampling came from island archipelagos, and therefore this type of SAR has been named the island SAR (Rosenzweig, 1995). A fundamental difference between nested and isolate SARs is that in nested SARs species number must always increase with the area size whereas in isolate SARs species number may increase or decrease with the area size.

The  $z$ -values of the SAR, key parameter to calculate extinction projections in [2], are often higher in oceanic islands than in nested areas in a continent. For instance, Rosenzweig (1995) gives a range of 0.25–0.35 for the former and 0.12–0.18 for the latter (Figure 2). However, recent studies have shown that the nested SAR exhibits a much broader range of  $z$ -values, from about 0.10 to more than 0.40 (Sala *et al.*, 2005; Drakare *et al.*, 2006), and that the  $z$ -values are particularly dependent on the scale of the study (Crawley and Harral, 2001; Pereira *et al.*, 2012). Furthermore, the  $z$ -value of isolates

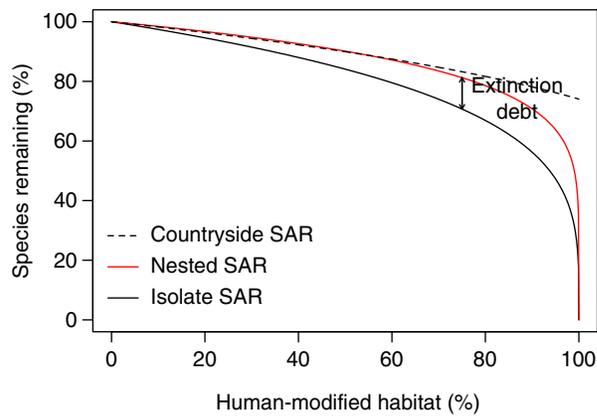


**Figure 1** The sampling scheme of the different types of species–area relationship: (a) nested sampling or continental SAR; (b) isolate sampling or island SAR.

on mainlands are often lower than the  $z$ -values of true islands in an ocean (Drakare *et al.*, 2006).

The species that are likely to go extinct immediately after habitat loss are the species endemic to the region of destroyed habitat (Kinzig and Harte, 2000; He and Hubbell, 2011). If the loss of the habitat happens in the periphery, then the nested SAR will describe the number of extinctions. This happens because the number of endemics in an outer ring of the habitat of size  $a$  is given by [2], assuming that the  $z$ -value of the SAR in [1] was estimated as in Figure 1(a) (Pereira *et al.*, 2012). If the habitat loss occurs in the center, the  $z$ -value from the nested SAR may overestimate the number of endemics. In that case,  $z_{\text{isolate}} = 0.25$  the endemics–area relationship (EAR), built by counting the number of endemics in progressively larger areas (as in Figure 1(a)), will better describe immediate species extinction. The  $z$ -values of the EAR are generally lower than the  $z$ -values of the nested continental SAR (He and Hubbell, 2011).

Many species that were not confined to the areas of habitat loss may go extinct in the long term because the remaining area of habitat may not be sufficient to allow for their persistence (i.e., sink species, as their dynamics are dominated by the modified habitats in the landscape which act as sinks). The difference between the species that go immediately extinct and the species that are likely to go extinct in the future has been coined “extinction debt.” This second stage of extinctions can take from decades to millennia (Pereira *et al.*, 2010), and it has been proposed that it is better described by the island SAR



**Figure 2** Comparison of the projections of species extinctions for the countryside SAR, the nested SAR and the isolate SAR. The EAR or the nested SAR (here  $z_{\text{nested}}=0.15$ ) follow a similar shape, but with lower  $z$ -values than the isolate SAR (here  $z_{\text{isolate}}=0.25$ ). Notice that when we use the classical SAR or the EAR all the species vanishes when the native habitat is completely lost. In the countryside SAR there are still species surviving when all the native habitat is converted. In this example we assumed that there are two groups of species (group 1 and 2) with the following parameters:  $h_{1,\text{Native}}=1$ ,  $h_{1,\text{Human-dominated}}=0.25$ ,  $h_{2,\text{Native}}=1$ ,  $h_{2,\text{Human-dominated}}=0.5$ ,  $c_1=0.75$ ,  $c_2=0.25$ , and  $z=0.25$ .

(Rosenzweig, 2001). This happens because the island SAR is more the result of colonization/extinction dynamics than of the sampling effects that are intrinsic to the nested SAR and instantaneous extinctions. Note that another process, habitat turn-over, plays a role in both the isolate SAR and the nested SAR. SAR for multiple habitats, discussed in the next section, allows the study of the effects of habitat turn-over on extinction.

One problem with using the island SAR is that a fragment of native habitat surrounded by agricultural areas is ecologically different from an island surrounded by oceans: the agricultural matrix is more inhabitable than an ocean for most species. An alternative is to use the SAR from habitat isolates (e.g., in agricultural land) to estimate extinctions. A problem with this second approach is that, in many cases, time after fragmentation is still relatively short for the communities in sampled habitat isolates to have reached equilibrium. A third problem comes from the difference between what happens when a large region of native habitat is reduced and what are the processes determining species diversity in habitat isolates of different sizes in an agricultural matrix. In the latter, there can be source-sink dynamics between different patches while in the former the only source is the original habitat region; therefore, instead of a spatial source-sink dynamics we have a temporal source-sink dynamics. The problem is further compounded by the fact that the remaining habitat is likely to be itself fragmented.

### Countryside Habitats: A Species–Area Relationship for Multiple Habitats

All of the SAR approaches described above assume that no species persist outside native habitats, and that when all

habitat is converted to human-dominated habitats (e.g., agricultural lands) all species go extinct (Figure 2). In reality many species are able to persist in human-dominated landscapes. For instance, at least half of terrestrial Costa Rican bird species and nonflying mammal species use agricultural habitats (Daily *et al.*, 2001, 2003). Pereira and Daily (2006) proposed a model to describe the use of both human-dominated and native habitats by many species: the countryside species–area relationship (countryside SAR).

The countryside SAR tracks the number of species in groups of species with similar affinities for the habitats in the landscape. The number of species in group  $i$ ,  $S_i$ , is given by

$$S_i = c_i \left( \sum_{j=1}^n h_{ij} A_j \right)^{z_i} \quad [3]$$

where  $h_{ij}$  is the affinity of group  $i$  to habitat  $j$ ,  $A_j$  is the area covered by habitat  $j$ , and  $n$  is the number of habitats. When the affinity of group  $i$  to the preferred habitat  $k$  is normalized to unity ( $h_{ik}=1$ ), the habitat affinity  $h_{ij}$  becomes a conversion factor from the area of habitat  $j$  into an equivalent area of preferred habitat. The total number of species in the landscape is given by

$$S = \sum_{i=1}^m S_i \quad [4]$$

where  $m$  is the number of species groups considered.

The countryside SAR can be used to project the biodiversity response to scenarios of land-use change (Proença *et al.*, 2009). In contrast with the classic SAR, a proportion of species may remain in the landscape even if all native habitat is converted to human-dominated habitats (Figure 2). The countryside SAR suggests that neither the isolate SAR nor the nested SAR describes extinctions. Instead, the equilibrium number of species in a modified landscape is higher than what is predicted by either of these two curves. Extinction debt may occur, but it will be given by the difference between immediate extinctions caused by habitat conversion (the endemic species that cannot survive in the new habitat, which will be fewer than the ones projected by the EAR) and the species that will go extinct in the medium to long-term because they do not have enough source habitats (i.e., sink species). The countryside SAR is likely to describe the short-term extinctions better, but more research is needed.

The countryside SAR can be used to project biodiversity changes, not only from the loss of native habitat but also from an increase in native habitats, such as natural forests (Proença *et al.*, 2009), or other habitats such as forest plantations, as long as those habitats are incorporated into the model and the affinities of species for those habitats are calculable. The countryside SAR [3] has been compared with the classic SAR [1] in mosaic landscapes with multiple habitats, both at the local scale (e.g.,  $< \text{km}^2$ , Proença *et al.*, 2009) and at the regional scale (e.g.,  $10^2$ – $10^4 \text{ km}^2$ , Martins *et al.*, 2011). In both cases the countryside SAR performed better than the classic SAR in describing the number of species in a given area, although the improvement was specially marked at the local scale.

There have been other models proposed for a multihabitat SAR (Tjørve, 2002; Triantis *et al.*, 2003). The model from Triantis *et al.* (2003) substitutes area in the SAR by the product of the area with the number of habitats. Tjørve's (2002) model adds the SAR of each habitat in the landscape deducted by the number of species overlapping between habitats to produce an estimate of the overall species diversity. None of the models explicitly tracks groups of species with distinct habitat affinities.

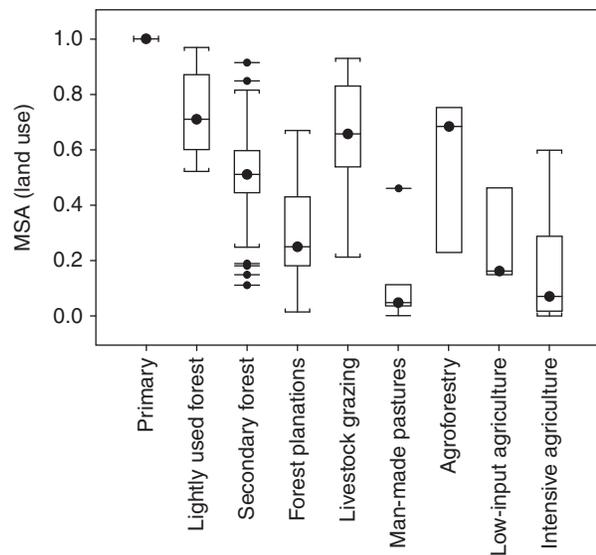
### Other Models

Here we discuss briefly three other classes of phenomenological models: direct inferences from geographic ranges, dose–response models and statistical estimators of diversity.

Global species distributions are now available for all terrestrial vertebrate groups (Mace *et al.*, 2005; Hoffmann *et al.*, 2010). Therefore, using the simple assumption that species are restricted to native habitats, the future range of a species can be estimated by obliterating from the species' current range all the areas that are projected to be converted to agriculture, according to spatially explicit scenarios of future land-use change (Jetz *et al.*, 2007). The declines in species ranges can then be classified according to the International Union for Conservation of Nature (IUCN) criteria to produce a list of future-threatened species (Jetz *et al.*, 2007). Projections that account for the persistence of species in human-dominated habitat can be obtained by classifying the suitability of the different land-uses for each species, and only obliterating from the current range of a species the area that will be occupied by habitat with no suitability for that species (Visconti *et al.*, 2011).

Dose–response models are based on correlations between the level of an ecosystem change driver and the biodiversity response. For instance, the GLOBIO model (Alkemade *et al.*, 2009) uses a matrix with estimates of changes in mean species abundances for conversions between any two types of land use, based on 89 empirical studies comparing species abundance between at least one land-use type and primary vegetation (Figure 3). Then, based on land-use change scenarios, GLOBIO projects changes in mean species abundance in each grid cell of the land-use maps, which can then be averaged over countries or regions. GLOBIO also uses relationships between the mean species abundance and other drivers such as the level of infrastructure development and the level of fragmentation, and assumes a multiplicative effect of the ecosystem change drivers to estimate the integrated impact on mean species abundance.

When sample plots are taken from a region, the total species diversity of the region can be estimated by using statistical estimators that use information on the number of plots in which each species was found. For instance, if the same species appear in all plots it is likely that all the species in the region were sampled. If most species occur in only one plot it is likely that many other rare species occur in the region and were not sampled, and therefore the species diversity of the region is higher than the number of species collected in the plots. Based on these statistical methods, Hughes *et al.* (2002) estimated the total number of bird species in a countryside region using samples from cattle pastures, coffee plots, mixed



**Figure 3** Box and whisker plot of the mean abundance of species (MSA) relative to their abundance in undisturbed/primary ecosystems for several land-use categories. Reproduced from Alkemade R, van Oorschot M, Miles L, Nellemann C, Bakkenes M, and ten Brink B (2009) GLOBIO3: A framework to investigate options for reducing global terrestrial biodiversity loss. *Ecosystems* 12: 374–390, with permission from Springer.

agricultural plots, gardens, thin riparian strips of native vegetation, and small forest remnants. Then, in order to test the effect of the disappearance of certain elements from the landscape, they recalculated the diversity of the species in the region without the plots corresponding to those elements.

### Process-Based Models

#### Reaction–Diffusion and Integro-Difference Equations

Reaction–diffusion models are spatially explicit models that track the population density of a species at each point in space. They were introduced in population ecology by Skellam (1951) and Kierstead and Slobodkin (1953), and are hereafter referred to as Skellam's equation (but sometimes also called the KISS model, after the name of these three authors). Earlier, reaction–diffusion had been introduced into population genetics by Fisher (1937), to look at the spatial spread of a mutant gene in a population. The main ingredients of Skellam's equation are the dispersal of individuals, which is approximated as a random diffusion process, and the local population growth dynamics (Shigesada and Kawasaki, 1997). For a population inhabiting habitat  $j$ , Skellam's equation is

$$\frac{\partial N(x,y,t)}{\partial t} = D_j \nabla^2 N(x,y,t) + F_j(N(x,y,t)) \quad [5]$$

where the symbol  $\nabla^2$  stands for  $(\partial^2/\partial x^2 + \partial^2/\partial y^2)$ ,  $N(x,y,t)$  is the density of the population, at location  $(x,y)$  at time  $t$ ,  $D_j$  is the diffusion coefficient in habitat  $j$  and  $F_j$  is the growth rate function of the population in  $j$  and it can take distinct forms. If we assume, for example, that the population has logistic growth in habitat  $j$  with growth rate  $r_j$  and carrying capacity

$K_j$ , then Skellam's equation becomes

$$\frac{\partial N(x,y,t)}{\partial t} = D_j \left( \frac{\partial^2 N(x,y,t)}{\partial x^2} + \frac{\partial^2 N(x,y,t)}{\partial y^2} \right) + r_j N(x,y,t) \left( 1 - \frac{N(x,y,t)}{K_j} \right) \quad [6]$$

This equation allows for the simulation of source-sink dynamics (Pulliam, 1988) between different habitats in the landscape (Figure 4(b)): the source habitats correspond to habitats where  $r_j > 0$  (i.e., the birth rate is higher than the death rate) and the sink habitats correspond to habitats where  $r_j < 0$  (i.e., the birth rate is lower than the death rate). The model predicts that there is a minimum area of source habitat required to sustain a species in a human-modified landscape (Pereira et al., 2004).

Skellam's equation is suited to describe the spatial and temporal evolution of a single species, but it can be generalized to communities of several species (Levin, 1974; Ökubo and Levin, 2001). For instance, Pereira et al. (2004) used Skellam's equation to study the response of the avifauna of Costa Rica to land-use change, and Pereira and Daily (2006) applied the same methodology to study the vulnerability of the mammal fauna of Central America in a countryside habitat. They applied Skellam's equation to each species individually using known population growth and diffusion coefficients from the literature or, when necessary, estimated them from allometric relationships. An important result of their work is that it is worth investing conservation resources in countryside habitats, in agreement with the results of the countryside SAR.

One of the advantage of Skellam's equation is its small number of parameters (at a minimum it involves three parameters: population growth rates in the source and sink habitats, and diffusion coefficient). In contrast, most models used in population viability analysis (Possingham et al., 2001) tend to be very parameter rich, turning them difficult to apply to a community of species (but see Keith et al., 2008). Still, Skellam's equation requires (and provides) more information than methods based on the SAR, because the latter assumes all

species to be equal (or in the case of the countryside SAR, all the species in a given group), therefore not taking into account their relative vulnerability to land-use change. Skellam's equation lies between the traditional (parameter poor) SAR and (parameter rich) population viability analyses.

There are, however, situations where the approximations implicit in Skellam's equation may not be reasonable, such as, when a species only reproduces and diffuses during specific periods of the year, or when diffusion coefficients are not appropriately modeled by normal distributions, such as when there are long distance dispersal events. In such cases, integro-difference equations are an alternative (Lewis, 1997; Hastings et al., 2005). For a population in habitat  $j$  with density or number of individuals  $N$ , where  $r_j$  is the growth rate function and  $k_j(x-x',y-y')$  is the dispersal probability between points  $(x',y')$  and  $(x,y)$  the integro-difference equation is

$$N_{t+1}(x,y) = \int_A k_j(x-x',y-y') r_j(N_t(x',y')) dx' dy' \quad [7]$$

where  $A$  is the area of habitat  $j$  and we kept  $t$  as a subscript to highlight the discrete temporal nature of the equation. Naturally, like Skellam's equation, integro-difference equations can also be applied to entire species communities, but so far we are not aware of such applications to countryside habitats.

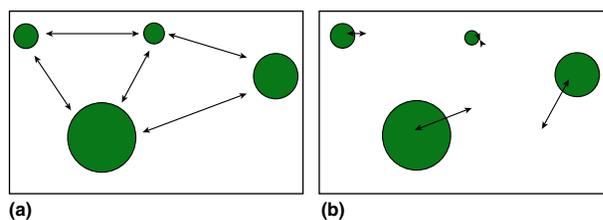
### Multispecies Metapopulation Analysis

Like Skellam's equation, metapopulation analysis was originally developed to study only one species. Levins (1969, 1970) developed the basic framework that was later considerably developed by authors such as Ilka Hanski (e.g., Hanski, 1999). The main idea of metapopulation analysis is to consider several populations of the same species inhabiting several patches, which are interconnected through dispersal, and determine how many patches are occupied at one time (Figure 4(a)). If the rates of colonization and extinction are  $c$  and  $e$ , respectively, and the fraction of occupied patches is given by  $P$  then the equation governing the time evolution of the fraction of occupied patches is

$$\frac{dP}{dt} = cP(1-P) - eP \quad [8]$$

If  $c-e > 0$ , the fraction of occupied patches reaches an equilibrium,  $P^* = (1 - e/c)$ . Naturally, this basic model can be refined. For instance,  $e$  and  $c$  can depend on the number of occupied patches, one can take into account the size of the patches and their explicit location, or one can consider patches of different "quality"

The metapopulation approach has definitely an appeal for studying countryside landscapes, because habitat loss and disturbance leads to populations inhabiting interconnected fragments, therefore following closely the premises of the metapopulation's theory framework. For example, Kuemmerle et al. (2011) used a metapopulation model to assess different strategies to establish (meta) populations of the European bison (*Bison bonasus*) in the Carpathians. However, in contrast with Skellam's model presented in the previous section, it assumes that the matrix (e.g., agricultural land) is only used for dispersal (Figure 4(a)). Notice that Skellam's model allows for the matrix to be used as sink habitat, and therefore tracks

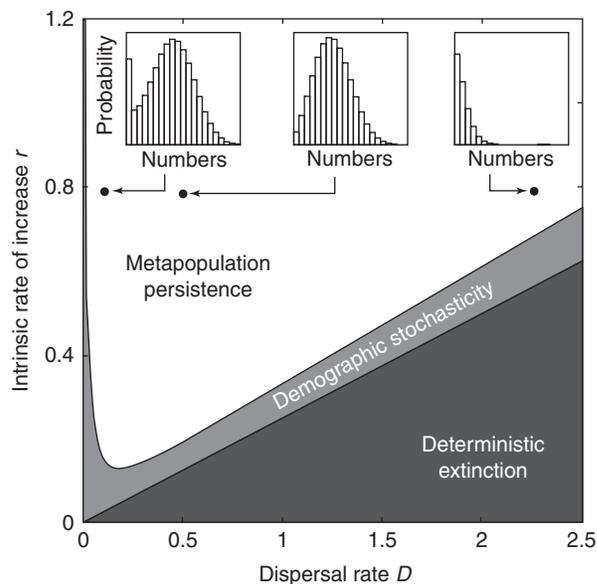


**Figure 4** Schematic representation of a metapopulation (a) and of the source-sink dynamics of the Skellam model (b). (a) The population occurs in the green patches, and each patch has a colonization rate (dependent on the distance to other patches) and an extinction rate (dependent on the size of the patch). (b) The population uses the entire landscape, but has a different fitness in each habitat. In a source habitat (green patches) birth rate is greater than mortality rate, while the reverse happens in the sink habitat (white matrix). The former case leads to dispersal ability being a positive factor to the survival of the population because more patches can be colonized. In the latter case dispersal may be detrimental because more individuals reach the sink habitat.

the source-sink dynamics of populations across the entire landscape (Figure 4(b)).

Another important difference between source-sink models and metapopulation models concerns the impact of dispersal ability. While in metapopulation analyses the role of dispersal is beneficial because individuals can colonize more patches, in reaction-diffusion models dispersal affects the population negatively because individuals tend to disperse away from good patches to sink habitats where population growth rates are negative (e.g., Borda-de-Água *et al.*, 2011). This disparity arises because the source-sink dynamics of Skellam's model are deterministic and the metapopulation models are stochastic. In a stochastic environment it may be advantageous to disperse to spread the risk between different patches, while in a deterministic environment dispersal is costly and tends to be disadvantageous (but see Hamilton and May, 1977 for a competitive benefit of dispersing individuals in a deterministic environment).

How do the relative costs and benefits of dispersal play out in fragmented landscapes or countryside habitats? Unfortunately, most metapopulation models ignore the population costs of dispersal and are unable to answer this question. Casagrandi and Gatto (1999) tackled this issue by developing a stochastic model that takes into account the number of individuals in each patch and, importantly, that takes into account dispersal mortality or inability to colonize. They show that only when dispersal rates are very small does the probability of persistence of the metapopulation increase, otherwise, the probability of extinction increases when dispersal increases (Figure 5).



**Figure 5** Population persistence (white area) as a function of the intrinsic rate of increase ( $y$ -axis) and dispersal rate ( $x$ -axis). When dispersal increases then the region of parameters where deterministic extinction occurs increases as well (dark-gray area). However for very small values of the dispersal rate ( $D < 0.25$ ) extinctions caused by demographic stochasticity decrease when the dispersal rate increases (light gray area). Reproduced from Casagrandi R and Gatto M (1999) A mesoscale approach to extinction risk in fragmented habitats. *Nature* 400: 560–562, with permission from Nature.

Most metapopulation studies focus on a single species, but metapopulation models have also been applied to communities of species (Nee and May, 1992; Tilman *et al.*, 1994; Marvier *et al.*, 2004). For example, Tilman *et al.* (1994) used a multispecies model to study the extinction debt in a fragmented landscape, and concluded that the most abundant species in an undisturbed habitat can be the most susceptible to extinction after habitat destruction. This happened because in their model there was a trade-off between being best competitor and best colonizer; hence, if fragmentation affects colonization, the species that had previously been the best competitors, and so the most abundant, became the most affected because of limitations to dispersal due to fragmentation. More recently, Keith *et al.* (2008) have integrated metapopulation models with bioclimatic envelope models to look at the response of a community of 234 plant species of the South African fynbos to climate change. They used age/stage-based matrix models to track the population size in each patch, and incorporated density dependence, environmental, and demographic stochasticity in the model, using the software RAMAS GIS (Akçakaya, 2000). A similar approach could be used to model the biodiversity dynamics of land-use change, where the bioclimatic envelope models and associated climate scenarios would be replaced by habitat suitability models applied to land-use change scenarios.

### Neutral Theory

While source-sink and metapopulation models were originally developed to study one species at the time, the neutral theory of biodiversity and biogeography (Hubbell, 2001) has at its core the relative abundance of species within a community. By “neutral” it is meant that all species in the same trophic level have the same probability of dying, reproducing, and speciating. Such an approximation has proved very controversial among ecologists (McGill, 2003; Clark, 2009), but the theory has inspired many recent studies in theoretical and applied ecology (for a review see Rosindell *et al.*, 2011). We should also point out that the classic Theory of Island Biogeography (MacArthur and Wilson, 1967) is also neutral because it assumes that all species are equal in their ability of dispersal, colonizing, and becoming extinct. An important difference, however, is that the Theory of Island Biogeography assumes neutrality at the species level, while neutral theory does it at the individual level and, as a consequence, the Theory of Island Biogeography can deal with species richness but not relative abundance.

In the original version laid out by Hubbell (2001), neutral theory considered two different scales: the local community corresponding to the local scale (e.g., the trees of a 50 ha plot of tropical rain forest), and the metacommunity corresponding to the regional scale (such as the Amazon basin). At both scales death and birth are part of the model, but while in the metacommunity speciation is the driving force providing new species (and, in the process, avoiding community dominance by a single species), in the local community that role is provided by migration of individuals from the metacommunity. According to the neutral theory model, at each time step an individual dies and is replaced with a new one. When

dealing with the local community, the new individual can be from a local species or an immigrant from one of the species in the metacommunity (that may or may not be present in the local community). The important characteristic of the theory is that all the processes are function of the species relative abundances; for example, if there is a migration event, the probability of choosing a species from the metacommunity is proportional to its abundance there. The evolution of the meta and local communities leads to the number of species and their relative abundance to reach an equilibrium value, characterized by the speciation and migration rates. This, however, is a dynamic equilibrium because species abundances drift over time; therefore, the species composition may change. It is only the number of species and their relative abundance that remain approximately constant.

Halley and Iwasa (2011) used a simplified version of neutral theory, by ignoring the immigration term, to estimate the time for accruing extinction debt in an isolated fragment. Under their model they derived the following diffusion equation:

$$\frac{\partial p}{\partial t} = \sum_{i=1}^{S-1} \frac{\partial^2}{\partial x_i^2} \left( \frac{x_i(1-x_i)}{N\tau} p \right) - \sum_{i=1}^{S-1} \sum_{j>i} \frac{\partial^2}{\partial x_i \partial x_j} \left( \frac{2x_i x_j}{N\tau} p \right) \quad [9]$$

where  $S$  is the number of species in the community,  $N$  the number of individuals in the habitat fragment,  $\tau$  is the mean generation time,  $x_i$  is the relative abundance of species  $i$ , and  $p(x_1, x_2, x_3, \dots, x_{S-1})$  is the distribution of the relative abundances for up to the last species, whose relative abundance is  $x_S = 1 - x_1 - x_2 - x_3 \dots - x_{S-1}$ . From this equation, they calculated the analytical expression for the time it takes for the number of species to reach half of its original size,  $S_0$ , as  $t_{50} = \tau N / S_0$ . The decay over time of the number of species is given by

$$S(t) = \frac{S_0}{1 + t/t_{50}} \quad [10]$$

Halley and Iwasa found very good agreement between their model and published empirical results for avifauna relaxation in fragments of intermediate size (100–100,000 ha), but noticed that the model broke down either for very small or very large areas, and hypothesized that this breakdown was due to the lack of immigration and speciation in their model.

Other studies have applied neutral models to estimate the number of tree species extinctions in the Amazon Basin for spatially explicit deforestation scenarios (Hubbell *et al.*, 2008), and to predict the rate of extinction of tree species in isolated fragments of the Amazon forest (Gilbert *et al.*, 2006).

## Concluding Remarks

There is now a wide range of models available to look at biodiversity dynamics on countryside landscapes. Process-based models require more parameters than phenomenological models, and therefore they have been mostly applied to local scales and to a single species or a small set of species. In contrast, phenomenological models may require as little as one parameter, and they have been applied to projecting

changes at global to regional scales for the total number of species. However, phenomenological models have also been used at the landscape scale, and there have been attempts to generalize and upscale the projections of process-based models. The type of projections needed (e.g., individual species vs. species groups, time to extinction vs. number of extinctions) and the data available are the key factors in determining the most appropriate model.

## Appendix

### List of Courses

1. Applied Ecology
2. Biodiversity and Ecosystem Services
3. Biodiversity and Global Changes
4. Environment and Land Planning
5. Population Resources and the Environment

*See also:* Biodiversity, Definition of. Conservation Biology, Discipline of. Dispersal Biogeography. Diversity, Community/Regional Level. Extinction in the Fossil Record. Island Biogeography. Land-Use Patterns, Historic. Loss of Biodiversity, Overview. Mammals, Conservation Efforts for. Metapopulations. Plant Conservation. Population Dynamics. Rainforest Loss and Change. Species–Area Relationships

## References

- Akçakaya HR (2000) Viability analyses with habitat-based metapopulation models. *Researches on Population Ecology* 42: 0045.
- Alkemade R, van Oorschot M, Miles L, Nellemann C, Bakkenes M, and ten Brink B (2009) GLOBIO3: A framework to investigate options for reducing global terrestrial biodiversity loss. *Ecosystems* 12: 374–390.
- Arrhenius O (1921) Species and area. *Journal of Ecology* 9: 95–99.
- Barnosky AD, Matzke N, Tomiya S, *et al.* (2011) Has the Earth's sixth mass extinction already arrived? *Nature* 471: 51–57.
- Borda-de-Água L, Navarro L, Gavinhos C, and Pereira HM (2011) Spatio-temporal impacts of roads on the persistence of populations: analytic and numerical approaches. *Landscape Ecology* 26: 253–265.
- Brook BW, Sodhi NS, and Ng PKL (2003) Catastrophic extinctions follow deforestation in Singapore. *Nature* 424: 420–423.
- Brooks TM, Pimm SL, and Oyugi JO (1999) Time lag between deforestation and bird extinction in tropical forest fragments. *Conservation Biology* 13: 1140–1150.
- Butchart SHM, Walpole M, Collen B, *et al.* (2010) Global biodiversity: indicators of recent declines. *Science* 328: 1164–1168.
- Casagrandi R and Gatto M (1999) A mesoscale approach to extinction risk in fragmented habitats. *Nature* 400: 560–562.
- Clark JS (2009) Beyond neutral science. *Trends in Ecology and Evolution* 24: 8–15.
- Crawley MJ and Hurrall JE (2001) Scale dependence in plant biodiversity. *Science* 291: 864–868.
- Daily GC, Ceballos G, Pacheco J, Suzan G, and Sanchez-Azofeifa A (2003) Countryside biogeography of neotropical mammals: Conservation opportunities in agricultural landscapes of Costa Rica. *Conservation Biology* 17: 1814–1826.
- Daily GC, Ehrlich PR, and Sanchez-Azofeifa GA (2001) Countryside biogeography: Use of human-dominated habitats by the avifauna of southern Costa Rica. *Ecological Applications* 11: 1–13.
- Dengler J (2009) Which function describes the species–area relationship best? A review and empirical evaluation. *Journal of Biogeography* 36: 728–744.

- Doak DF (1995) Source-sink models and the problem of habitat degradation: General models and applications to the Yellowstone grizzly. *Conservation Biology* 9: 1370–1379.
- Drakare S, Lennon JJ, and Hillebrand H (2006) The imprint of the geographical, evolutionary and ecological context on species–area relationships. *Ecology Letters* 9: 215–227.
- Duraiappah A, Naheem S, Agardy T, et al. (2005) *Ecosystems and Human Well-Being: Biodiversity Synthesis*. Washington, DC: World Resources Institute.
- FAO (2010) *Global Forest Resources Assessment 2010*. Rome: Food and Agriculture Organization of the United Nations.
- Fisher RA (1937) The wave of advance of advantageous genes. *Annals of Human Genetics* 7: 355–369.
- Gilbert B, Laurance WF, Leigh EG, and Nascimento HEM (2006) Can neutral theory predict the responses of amazonian tree communities to forest fragmentation? *American Naturalist* 168: 304–317.
- Halley JM and Iwasa Y (2011) Neutral theory as a predictor of avifaunal extinctions after habitat loss. *Proceedings of the National Academy of Sciences of the United States of America* 108: 2316–2321.
- Hamilton WD and May RM (1977) Dispersal in stable habitats. *Nature* 269: 578–581.
- Hanski I (1999) *Metapopulation Ecology*. Oxford, UK: Oxford University Press.
- Hastings A, Cuddington K, Davies KF, et al. (2005) The spatial spread of invasions: New developments in theory and evidence. *Ecology Letters* 8: 91–101.
- He F and Hubbell SP (2011) Species–area relationships always overestimate extinction rates from habitat loss. *Nature* 473: 368–371.
- Hoffmann M, Hilton-Taylor C, Angulo A, et al. (2010) The impact of conservation on the status of the World's vertebrates. *Science* 330: 1503–1509.
- Hubbell SP (2001) *The Unified Neutral Theory of Biodiversity and Biogeography*. Princeton, NJ: Princeton University Press.
- Hubbell SP, He FL, Condit R, Borda-de-Agua L, Kellner J, and ter Steege H (2008) How many tree species and how many of them are there in the Amazon will go extinct? *Proceedings of the National Academy of Sciences of the United States of America* 105: 11498–11504.
- Hughes JB, Daily GC, and Ehrlich PR (2002) Conservation of tropical forest birds in countryside habitats. *Ecology Letters* 5: 121–129.
- Jetz W, Wilcove DS, and Dobson AP (2007) Projected impacts of climate and land-use change on the global diversity of birds. *PLoS Biology* 5: e157.
- Keith DA, Akcakaya HR, Thuiller W, et al. (2008) Predicting extinction risks under climate change: Coupling stochastic population models with dynamic bioclimatic habitat models. *Biology Letters* 4: 560–563.
- Kierstead H and Slobodkin LB (1953) The size of water masses containing plankton boom. *Journal of Marine Research* 12: 141–147.
- Kinzig A and Harte J (2000) Implications of endemics–area relationships for estimates of species extinctions. *Ecology* 81: 3305–3311.
- Kuemmerle T, Perzanowski K, Akcakaya HR, et al. (2011) Cost-effectiveness of strategies to establish a European bison metapopulation in the Carpathians. *Journal of Applied Ecology* 48: 317–329.
- Levin SA (1974) Dispersion and population interactions. *American Naturalist* 207–228.
- Levins R (1969) Some demographic and genetic consequences of environmental heterogeneity for biological control. *Bulletin of The Entomological Society of America* 15: 237–240.
- Levins R (1970) Extinction. *Lectures on Mathematical Analysis of Biological Phenomena* 231: 123–138.
- Lewis MA (1997) Variability, patchiness, and jump dispersal in the spread of an invading population. In: Tilman D and Kareiva PM (eds.) *Spatial Ecology: The Role of Space in Population Dynamics and Interspecific Interactions*, pp. xiv, 308. Princeton, NJ: Princeton University Press.
- MacArthur RH and Wilson EO (1967) *The Theory of Island Biogeography*. Princeton, NJ: Princeton University Press.
- Mace GM, Masundire H, Baillie J, et al. (2005) Biodiversity. In: Hassan R, Scholes B, and Ash N (eds.) *Ecosystems and Human Well-being: Current State and Trends: Findings of the Condition and Trends Working Group of the Millennium Ecosystem Assessment*, pp. 77–126. Washington, DC: Island Press.
- Martins IS (2009) *What Is the Relationship between Habitat Diversity and Species Diversity from the Local to the Regional Scale?* Masters Thesis, Universidade de Lisboa, Portugal.
- Marvier M, Kareiva P, and Neubert MG (2004) Habitat destruction, fragmentation, and disturbance promote invasion by habitat generalists in a multispecies metapopulation. *Risk Analysis* 4: 869–878.
- McGill B (2003) A test of the unified neutral theory of biodiversity. *Nature* 422: 881–885.
- Nee S and May RM (1992) Dynamics of metapopulations – habitat destruction and competitive coexistence. *Journal of Animal Ecology* 61: 37–40.
- Ôkubo A and Levin SA (2001) *Diffusion and Ecological Problems: Modern Perspectives*. New York, NY: Springer.
- Pereira HM, Borda-de-Agua L, and Martins IS (2012) Geometry and scales in species–area relationships. *Nature* 482: E3–E4.
- Pereira HM and Daily GC (2006) Modeling biodiversity dynamics in countryside landscapes. *Ecology* 87: 1877–1885.
- Pereira HM, Daily GC, and Roughgarden J (2004) A framework for assessing the relative vulnerability of species to land-use change. *Ecological Applications* 14: 730–742.
- Pereira HM, Leadley PW, Proenca V, et al. (2010) Scenarios for global biodiversity in the 21st century. *Science* 330: 1496–1502.
- Pimm SL, Russell GJ, Gittleman JL, and Brooks TM (1995) The future of biodiversity. *Science* 269: 347–350.
- Possingham H, Lindenmayer DB, and McCarthy MA (2001) In: Levin S (ed.) *Population Viability Analysis. Encyclopedia of Biodiversity*, pp. 831–843. San Diego, California, USA: Academic Press.
- Proença VM (2009) *Galicio-Portuguese Oak Forest of Quercus Robur and Quercus Pyrenaica: Biodiversity Patterns and Forest Response to Fire*. PhD Thesis, Universidade de Lisboa, Portugal.
- Pulliam HR (1988) Sources, sinks, and population regulation. *American Naturalist* 132: 652–661.
- Ranganathan J, Daniels R, Chandran M, Ehrlich P, and Daily G (2008) Sustaining biodiversity in ancient tropical countryside. *Proceedings of the National Academy of Sciences of the United States of America* 105: 17852–17854.
- Rosenzweig ML (1995) *Species Diversity in Space and Time*. Cambridge, UK: Cambridge University Press.
- Rosenzweig ML (2001) Loss of speciation rate will impoverish future diversity. *Proceedings of the National Academy of Sciences of the United States of America* 98: 5404–5410.
- Rosindell J, Hubbell SP, and Etienne RS (2011) The unified neutral theory of biodiversity and biogeography at age ten. *Trends in Ecology & Evolution* 26: 340–348.
- Sala OE, van Vuuren D, Pereira HM, et al. (2005) Biodiversity Across Scenarios. In: Carpenter SR, Prabhu LP, Bennet EM, and Zurek MB (eds.) *Ecosystems and Human Well-Being: Scenarios: Findings of the Scenarios Working Group of the Millennium Ecosystem Assessment*, pp. 375–408. Washington, DC: Island Press.
- Shigesada N and Kawasaki K (1997) *Biological Invasions: Theory and Practice*. Oxford: Oxford University Press.
- Skellam JG (1951) Random dispersal in theoretical populations. *Biometrika* 38: 196–218.
- Thuiller W, Albert C, Araujo M, et al. (2008) Predicting global change impacts on plant species' distributions: Future challenges. *Perspectives in Plant Ecology Evolution and Systematics* 9: 137–152.
- Tilman D, May R, Lehman CL, and Nowak MA (1994) Habitat destruction and the extinction debt. *Nature* 371: 65–66.
- Tjørve E (2002) Habitat size and number in multi-habitat landscapes: A model approach based on species–area curves. *Ecography* 25: 17–24.
- Triantis KA, Mylonas M, Lika K, and Vardinoyannis K (2003) A model for the species–area–habitat relationship. *Journal of Biogeography* 30: 19–27.
- UNEP (2007) *Global Environment Outlook 4*. Nairobi, Kenya: UNEP.
- Visconti P, Pressey RL, Giorgini D, et al. (2011) Future hotspots of terrestrial mammal loss. *Philosophical Transactions of the Royal Society B: Biological Sciences* 366: 2693–2702.
- van Vuuren D, Sala O, and Pereira HM (2006) The future of vascular plant diversity under four global scenarios. *Ecology and Society* 11: 25.
- Wright S (2010) The future of tropical forests. *Year in Ecology and Conservation Biology 2010* 1195: 1–27.