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Extending Hubbell's neutral theory of biodiversity using a
demographic model

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הריני מאשר את הנושא ואת התוכנית, ומסכים להדריך את המועמד בביצוע עבודה זו:

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Abstract

Understanding the mechanisms controlling the diversity of ecological communities is one of the oldest and most challenging questions in ecology. Hubbell's 'unified neutral theory of biodiversity' (Hubbell 2001) is the most ambitious attempt to date to develop a general theory in ecology, and has been regarded as "one of the most important contributions to ecology and biogeography of the past half century" (E.O. Wilson). However, Hubbell's theory, as well as its more recent extensions, relies on three unrealistic assumptions: constant community size; a 'zero-sum game' where each death is immediately replaced by a new individual; and strict among-species similarity in vital rates (Hubbell 2001, McKane et al. 2004, Volkov et al. 2003, Etienne and Alonso 2005). These fundamental assumptions contrast our knowledge about the nature of ecological communities and are only made for analytical simplicity. In my Ph.D research I propose to develop a new model of species diversity that will relax all three assumptions. The model will be individual-based and the dynamics of the community will be derived from fundamental processes of reproduction, mortality, and immigration, modeled with explicit rates.

In contrast to Hubbell's theory where community size is a free parameter, in my model community size will be derived from the same processes that govern the abundance of individual species. Hubbell's assumption of strict similarity in vital rates will be replaced by the assumption of fitness equivalence (similarity in overall fitness) which is much more realistic. The model will incorporate trade-offs in per-capita rates of reproduction and mortality, one of the most fundamental concepts of community ecology (MacArthur and Wilson 1967, Grime 1979). In spite of adding these complexities (which make the model more realistic than existing theories), I will provide an analytic solution of the model. I will also analyze a wide spectrum of factors that are known to affect species diversity such as the properties of the regional species pool, habitat heterogeneity, habitat loss, and variation in productivity. All of these factors will be analyzed analytically, using extensions of the basic model. The new model will provide a significant improvement for current theories of species diversity and I expect that it will lay the ground to a new generation of analytically tractable models of community dynamics that will be much more general and realistic than existing models.

Background

The fast changes that take place in our world, the vast majority due to human influences, require in-depth understanding of their consequences to ecological communities. The 2004 IUCN red list contains over 15000 species at a risk of extinction in the near future, including one in three species of amphibians (32%), one in four species of mammals (23%) and one in eight species of birds (12%).

Community ecology aims to study the distribution, abundance, demography and interactions of populations of different species within communities. Hubbell's (2001) 'unified neutral theory of biodiversity and biogeography' is a recent attempt to develop a general theory in community ecology which has already been regarded as "one of the most important contributions to ecology and biogeography of the past half century" (E.O. Wilson). The theory is causing a major conceptual shift in ecology by emphasizing the role of stochasticity and neutral processes in the regulation of ecological communities (Whitfield 2002, Chave 2004, see also a series of papers in a special feature on neutral community ecology published in Ecology, issue 87(6)).

Two fundamental concepts of Hubbell's (2001) neutral theory are 'zero-sum' dynamics and random drift of species abundances. The concept of zero-sum dynamics implies that each death event in the community is immediately replaced by a new individual, either from an outer mainland or by birth of an offspring in the local community. Random drift is present, as (1) the species of the replaced individual, as well as that of the replacing offspring or immigrant, are randomly drawn according to the relative abundances of species in the source community (the local community or the outer mainland, respectively), and (2) the source of the new individual, being an offspring from the local community or an immigrant from the outer mainland, is also determined randomly.

Hubbell's model in detail

Hubbell describes a stochastic, individual-based, 'mainland-island model' (*sensu* Hanski 1999) where all individuals of all species are demographically equivalent (Hubbell 2001). The mainland community is regulated by evolutionary processes (speciation and extinction) and provides immigrants to the island community which is regulated by much faster processes of local reproduction, mortality, and immigration. I will mainly focus on the dynamics of the island community.

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The island is conceptualized as a spatially-implicit landscape that consists of J sites with each site being able to support at most one individual. The community is 'saturated' in the sense that all sites are continuously occupied, and the dynamics is modeled as a 'zero-sum game' in the sense that each time step, a single, randomly drawn individual is killed and is immediately replaced by a new individual. The replacing individual is either an offspring of a randomly drawn individual from the local community (with probability 1-m), or a randomly drawn immigrant from the mainland (with probability m). The likelihood of each species to replace a death event is determined by its relative abundance in the source community from which the replacing individual is drawn. Dispersal is assumed to be global so that each site is accessible from any other site.

Under the assumption of the zero-sum game, the dynamics of a single species in the local (island) community is given by:

(1) $\quad W(N-1 \mid N) = (1-m) \dfrac{N}{J} \dfrac{(J-N)}{J-1} + m \dfrac{N}{J}(1-P_j^{reg})$

$\qquad W(N+1 \mid N_j) = (1-m) \dfrac{(J-N)}{J} \dfrac{N}{J-1} + m \dfrac{(J-N)}{J} P_j^{reg}$

where m is the probability of replacement by an immigrant, N is the number of individuals of species j, J is the size of the local community, and P_j^{reg} is the relative abundance of species j in the mainland community (Hubbell 2001). The probability that species j will have N individuals in a local community undergoing Hubbell's (2001) zero-sum game is given by (McKane et al. 2000, 2004, Vallade and Houchmandzadeh 2003, Volkov et al. 2003):

(2) $\quad P_j^{local}(N) = \begin{pmatrix} J \\ N \end{pmatrix} \dfrac{B(N+P^\wedge, N^* - N)}{B(P^\wedge, N^* - J)}$

where $B(a,b) = \Gamma(a)\Gamma(b)/\Gamma(a+b)$, $P^\wedge = \dfrac{m(J-1)}{(1-m)} P_j^{reg}$ and $N^* = \dfrac{J-m}{1-m} - P^\wedge$.

A central requirement in this model is the zero-sum game. Hubbell makes an unrealistic assumption that communities are saturated and do not change in size, and that individuals have infinite rates of birth and immigration, so that each available site due to the death of an individual is immediately taken by a new individual. This assumption contrasts a fundamental result from models of metapopulation dynamics such as those of Levins (1969, 1970) and its derivatives (Hastings 1980, Tilman 1994,

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Tilman et al. 1997), which show that species never occupy all available sites. A desired extension of the model is therefore the ability to infer species abundance distribution and species richness for unsaturated communities, in which a death is not immediately replaced by birth or immigration, and there is a temporal variability in community size. Recent papers have relaxed Hubbell's unrealistic assumptions (Volkov et al. 2003, 2005, He 2005, Etienne et al. 2007), but they are based on a very problematic assumption, namely, that each species in the community is totally independent of all other species. This assumption seems as unrealistic as Hubbell's original assumption of a 'zero-sum dynamics'.

Another major source of criticism against Hubbell's model is its assumption of 'strict' neutrality, i.e. neutrality in the per-capita probability of death, birth and immigration. Differences among species in reproduction, mortality, dispersal, and competitive ability are clearly evident, and trade-offs among them are a major concept in the study of species coexistence. Although Hubbell limits his model to functionally-equivalent species in a homogeneous environment, he himself does not ignore the importance of life-history trade-offs among species, but rather argues that "life history *trade-offs* equalize the per capita relative *fitness* of species in the community" (Hubbell 2001). A useful extension to Hubbell's model is therefore replacing its assumption of strict neutrality with neutrality in overall fitness.

The neutral theory of biodiversity has gained considerable popularity as a null model for community dynamics (Bell 2000, Maurer and McGill 2004, Nee 2005, Alonso et al. 2006, Gotelli and McGill 2006). Nonetheless, in its current formulation, the theory is not applicable to studies of complex ecological phenomena, such as habitat loss, environmental heterogeneity, and variation in productivity. All of these factors are known to play an important role in determining the diversity of ecological communities (Hutchinson 1957, MacArthur 1972, Abrams 1995, Ehrlich 1988, Fahrig 1997). Thus, there is a need to extend the framework of Hubbell's model to allow the incorporation of such key determinants of species diversity.

Research objectives

The main goal of my research is to develop a new model of community dynamics that will extend the scope of the neutral theory of biodiversity, thereby increasing its capabilities as a null model for community ecology. This will be done in several directions:

1. Relaxing the assumption of community saturation
2. Connecting Hubbell's model and the model of Levins, one of the leading models for metapopulation dynamics, thereby reconciling apparent contradictions between them
3. Replacing the assumption of strict neutrality with neutrality in fitness
4. Allowing incorporation of complex ecological phenomena into the extended model, while still maintaining a simple analytically-tractable framework

Specifically, I propose to develop an individual-based model, in which the dynamics of the overall community is derived from fundamental processes of reproduction, mortality, and immigration, modeled with explicit rates. Such an approach better connects the model to the fundamental demographic processes that shape communities, and offers a major methodological advantage over the model of Hubbell, which does not include explicit representation of demographic rates. I will build a simulation tool for the model using computer code. I will also provide analytic tools to study the dynamics of the model. The analytic treatment will provide more profound understanding of the mechanisms governing species richness.

The demographic model to be developed will provide a unified framework for the evaluation of a number of leading theories of community ecology, including the theory of island biogeography (MacArthur and Wilson 1967), the theory of patch dynamics (Levins 1969), niche theory (Hutchinson 1957) and the neutral theory of biodiversity (Hubbell 2001). A unified framework would prove highly useful in determining the relative importance of these variable concepts and in reconciling apparent contradictions between existing theories.

Methods

The basic demographic model

The basic demographic model relaxes Hubbell's assumptions of community saturation and zero-sum game. It is an individual-based, spatially-implicit model of a neutral community of sessile organisms. As in Hubbell (2001) I limit the definition of community to a group of trophically similar species that are limited by the same resources. The model describes the dynamics of a local community that receives immigrants from a regional species pool (MacArthur and Wilson 1967, Bell 2000, Hubbell 2001). Individuals in the local community compete for vacant sites in a spatially implicit landscape consisting of A sites, where each site can be occupied by at most one individual. Each individual, regardless of its species identity, dies at rate e and gives birth to one offspring at rate c. A new offspring is immediately dispersed into a random site. Immigration of immigrants of the j'th species from the regional species pool to each site in the landscape occurs at a rate iP_j^{reg}, where P_j^{reg} is the abundance of the j'th species in the regional species pool. Dispersed offspring and immigrants can only establish in vacant sites. The community is neutral, in the sense that individuals of all species have the same birth, death, and immigration rates. The overall dynamics is modeled as a continuous-time Markov process (McKane et al. 2004, Etienne and Alonso 2005) where at most one event (birth, death, or immigration) occurs at each time step.

Numerical simulations

I will create a simulation tool using computer code to numerically simulate the dynamics of the model. The results of the numerical simulations will aid me in providing an analytic solution to the model, by serving as a reference point for the analytic results. I will additionally use numerical simulations where an analytic solution will not be obtained.

Modelling design. I will model the landscape as a collection of A sites, each able to hold at most one individual. I will record the state of each site (whether vacant or occupied) and, if occupied, the identity of the species it holds. The landscape will be initialized with a random set of individuals of different species, and will be run until the system reaches equilibrium. I will then record community size, species richness and the abundance of each species in the local community. The model will

include explicitly events of birth, death and immigration at the corresponding rates c, e, and i.

Unlike the forced coupling between an event of death and an event of birth in Hubbell's model (the 'zero-sum game'), in my model the order of events is fully stochastic. The occurrence times of events with a given rate x are described by a Poisson process with the parameter x. For computational efficiency, instead of modelling two Poisson processes of birth and death for each individual and another Poisson process of immigration for each site, I will use the method of 'thinning of a Poisson process' (Durrett 1995, Berec 2002) which keeps only one background Poisson process.

Initial conditions. Initially, the landscape will be filled with individuals of various species, randomly selected according to the metacommunity abundance. I will test several mainland distributions to study the effect of variation in the number of species and the abundance distribution of individual species in the regional species pool on local richness. I will mainly use a mainland community consisting of a large number of species (several hundreds) with varying abundances roughly following a log-series distribution, generated using Ewens' sampling formula (Ewens 1972, Hubbell 2001) using J_M (number of individuals if the mainland community) of 10,000,000 and θ (biodiversity number) of 20.

Results acquisition. I will allow the system to reach equilibrium by running the simulations for 100,000 time-steps, and will then record various statistics in 1,000 sampling points, taken every 50 time-steps, to a total of 50,000 time-steps, and will calculate the average of these 1,000 records. I will monitor community size, species richness and the abundance of each species in the local community.

Parameters used. In the proposed model all species have equal per-capita rates of birth, death and immigration ability. I will test several values of birth, death and immigration rates and of total area, in order to study their effects on species richness. Each set of parameters will be run several times, and mean values and standard deviations of each parameter set will be recorded.

Analytic treatment

I will provide an analytic solution to my model using tools from the theory of Markov chains. The solution will give the distribution of community size, species

richness and species abundance in my model. Analytic treatment cancels the need to resort to time-consuming computer simulations, and provides more profound understanding of the mechanisms governing the behavior of the model. Relaxing the assumption of constant community size exponentially increases the number of possible states, and highly complicates the analytic treatment. I will first study the distribution of community size at equilibrium (see *"Preliminary results"*) and then connect the model to the model of Levins (1969, 1970) and that of Hubbell (2001). I argue that the size of the community in the proposed model is well approximated by a modification of model of Levins (1969, 1970), while the distribution of species abundance is well approximated by the model of Hubbell (2001) (see *"Reconciling the contradiction between the Levins model and Hubbell's neutral theory of biodiversity"* for more information on this).

Relaxing the assumption of community saturation

In the demographic model community size is governed by the same processes that govern species abundance – an increase in the abundance of a species due to local reproduction or immigration also increase community size, while a decrease due to mortality decreases community size. While in Hubbell's model community size is given as an input parameter, in my model community size will be explicitly derived from the demographic rates and the local area. I therefore predict that, in my model, the community might be saturated or unsaturated, depending on the balance between the rates of reproduction, mortality, and immigration. Therefore, as a first stage I will study how differences in the demographic rates influence the distribution of community size and what are the consequences of variation in community size for species richness.

Reconciling the contradiction between the Levins model and Hubbell's neutral theory of biodiversity

The most fundamental assumption of Hubbell's model is the assumption that ecological communities are *always* saturated and unoccupied sites never exist. This contrasts a universal rule derived from Levins' metapopulation model (1969, 1970) and similar patch-occupancy models (Holyoak et al. 2005). The multi-species formulation of the classic Levins model (Tilman 1994, Hastings 1980, Kondoh 2001) is a deterministic, spatially implicit model of community dynamics, where the

landscape is modeled as an infinite collection of sites, each able to support a single individual. Dispersal is assumed to be global, so that any site is accessible from any other site. Analysis of this model indicates that any stable equilibrium is associated with some fraction of empty sites, implying that ecological communities are never saturated (Hastings 1980, Tilman 1994, Tilman et al. 1997). In my work I will incorporate the basic elements of the two theories in an attempt to reconcile this apparent contradiction. Specifically, I shall develop a 'hybrid' model where the size of the community is determined using a modification of Levins' model, and the number and relative abundance of individual species are determined by random drift using Hubbell's model. Levins' model can be used to calculate the size of the overall community because in a neutral community, all species have the same demographic rates and can therefore be modeled as a single 'population'. This hybrid model can be considered as a mean-field approximation to my basic demographic model because community size is derived from the actual demographic parameters assuming an infinite area. The hybrid model will allow me to derive the input parameters of Hubbell's model, namely community size and the probability of replacement by an immigrant, from the demographic processes that determine them (see *preliminary results*), and will provide a unified framework that captures the main elements of both Levins' and Hubbell's models.

Neutrality in fitness

In the next step I will extend the model by relaxing the assumption of strict neutrality, i.e. neutrality in the per-capita rates of birth, death and immigration. In this extended version of the model species will differ in their per-capita demographic rates. Individuals of species j will reproduce at rate c_j, die at rate e_j and immigrate at rate i_j. Still, species will be ecologically equivalent in their overall fitness, so that c_j/e_j and i_j/e_j are equal among all species. This definition of neutrality is much more realistic than Hubbell's (2001) assumption of strict neutrality in *per-capita* vital rates (Chave 2004) and allows trade-offs between reproduction and mortality rates. I will incorporate this extension of the basic model into the numerical simulations, and provide analytical derivation of its results. In addition I attempt to test other forms of trade-offs, e.g. competition-colonization trade-offs (Levins and Culver 1971, Slatkin 1974, Hastings 1980, Tilman 1994, Yu and Wilson 2001) using numerical simulations

and possibly analytical approximations in order to evaluate how such trade-offs affect the results of my basic demographic model. This analysis will allow me to test the importance of fitness equivalence in structuring ecological communities and to relate my results to theories of species diversity based on competition-colonization trade-offs.

The proposed model as a demographic formulation of island biogeography theory

The proposed demographic model will allow a deeper understanding of predictions made by the theory of island biogeography (MacArthur and Wilson 1967) and its recent formulation as the unified theory of biodiversity (Hubbell 2001). Both theories focus on the effects of area and immigration as the main determinants of species richness, but neither of the theories really investigates the fundamental demographic mechanisms by which variation in area or immigration affect the number of species in the community. MacArthur and Wilson's (1967) model does not allow such appreciation because it is formulated in terms of species-level processes (colonization and extinction) rather than demographic processes as the basic drivers of species diversity. Hubbell's model does not allow such appreciation, as it implicitly assumes infinite fecundity and does not include explicit representation of birth, death and immigration rates. The model I propose provides a full demographic formulation of the theory of island biogeography, and allows me to study the fundamental mechanisms by which area and immigration affect the diversity of ecological communities. Thus, in my formulation, the basic parameters of classical island biogeography theory (colonization and extinction), and of the unified neutral theory of biodiversity (J, community size, and m, the probability of an empty site being occupied by a new immigrant) will emerge as 'emergent properties' from the underlying demographic processes that govern the dynamics of the community.

It should be noted that in Hubbell's formulation, J and m are treated as free, independent parameters. It is simple to see that in my model these parameters are not independent because both the size of the community and the probability of a site being occupied by a new immigrant are influenced by the basic demographic parameters. I therefore expect that my model will provide different and more realistic predictions than those obtained from Hubbell's model.

Further applications of the model

An important application of neutral models is as null models (Bell 2001, Maurer and McGill 2004, Nee 2005, Alonso et al. 2006, Gotelli and McGill 2006). The incorporation of the fundamental demographic processes in my model will allow me to use the model as a null model for studying a variety of key ecological factors, for which Hubbell's model is not applicable. I briefly describe here several possible extensions that I hope to include in an extended model.

Habitat heterogeneity is considered by almost any theory in community ecology one of the most fundamental diversity-maintenance mechanisms. The common notion is that habitat heterogeneity increases species richness by providing more 'niches' and increasing intraspecific competition over interspecific competition (Hutchinson 1957, MacArthur 1972, Petren 2001, Silvertown 2004). However, very few studies have incorporated habitat heterogeneity in models of community dynamics and even fewer studies have systematically analyzed the demographic mechanisms by which habitat heterogeneity affects the number of species in a community. I incorporate habitat heterogeneity into the basic model by assigning each site into one of H different habitats. To keep the model 'neutral' at the overall community level each species is able to persist in only one, 'source' habitat, each habitat consists of an equal number of sites, and the various habitats have a fixed number of different (non-overlapping) species with the same abundance distribution. This extension provides a null model for testing and interpreting observed responses of species richness to habitat heterogeneity. Analyses show that such a model provides unexpected results that differ from predictions of existing theories (Kadmon and Allouche 2007).

Productivity has long been considered a major determinant of species richness but the exact mechanisms underlying the observed productivity-diversity relationships are still highly debated (Abrams 1995, Mouquet et al. 2002, Chase and Leibold 2002). Recently it has been shown (Kadmon and Benjamini 2006) that neutral interactions can generate positive, negative, and unimodal relationships between species richness and productivity (Fig. 2 in their manuscript). This result is consistent with empirical data (Waide et al. 1999, Mitelbach et al. 2001), but contrasts the widely accepted notion that unimodal and negative productivity-diversity relationships require tradeoffs or differences in competitive ability among species (Grime 1973, Huston 1979, Rosenzweig and Abramski 1993, Tilman and Pacala 1993). I intend to verify

the result of Kadmon and Benjamini (2006) by incorporating productivity into my demographic model. Under the simplest scenario, increased productivity is expected to increase local reproduction (Kondoh 2001, Kadmon and Benjamini 2006). I will therefore define local reproduction as a function of productivity, and test its effects on community dynamics and species richness.

Habitat loss is often recognized as the greatest threat to biodiversity (Ehrlich 1988, Fahrig 1997) but previous models have generated contrasting predictions concerning the manner by which increasing habitat loss affects the number of species in a community (Tilman et al. 1994, 1997, Ney-Nifle and Mangel 2000, Kinzig and Harte 2000, Sole et al. 2004) - a continuous, gradual loss of species, or a long delay followed by a sharp decrease in species richness. All of these models show that habitat loss greatly reduces the size of the community. Since in Hubbell's model community size is given as an input parameter, Hubbell's model is not suitable to study the effect of habitat loss on species richness. My model allows incorporating such an effect because community size is determined by the basic demographic rates and the number of sites suitable for establishment. I will incorporate habitat loss into the model by setting a portion of the sites as inhabitable, so that local offspring and immigrants that arrive to these sites are unable to establish and die. Based on preliminary analyses I expect that the model will be capable of generating both gradual responses and delays followed by a sharp decrease in species richness, depending on the balance between the various demographic rates.

The relationship between local and regional species diversity has attracted the attention of ecologists due to the increasing interest in the degree to which local species diversity is limited by local vs. regional processes (Srivastava 1999, He et al. 2005). While other views have been suggested, it has widely been hypothesized that curvilinear ('saturated') local-regional diversity relationships indicate limitation by local interactions, while linear relationships imply limitation by low immigration from the regional species pool (Terborgh and Faaborg 1980, Cornell and Lawton 1992, Srivastava 1999). The demographic model I propose will allow me to test this hypothesis by analyzing the response of local species richness to manipulations of the regional species pool. This will be done for varying levels of reproduction, mortality, immigration and area, in order to test whether and how differences in demography and area affect the local-regional diversity relationship.

A unified framework of community ecology

The proposed demographic model can be used as a unified framework for a number of leading theories of species diversity. It includes random drift and neutrality among species, as in the neutral theory of biodiversity (Hubbell 2001). It is demographically-based and allows trade-offs in species properties, as in multi-species versions of the theory of patch dynamics (Tilman 1994, Loreau and Mouquet 1999). Species richness is determined by the balance between processes of extinction and recolonization, and is affected by local area and geographic isolation, as in the theory of island biogeography (MacArthur and Wilson 1967). The extended model will incorporate habitat heterogeneity and niche differentiation, as emphasized by niche theory (Hutchinson 1957), and will enable to evaluate previous theories concerning the potential consequences of habitat loss. These capabilities will enable me to use the model as a tool for synthesizing existing concepts of species diversity and reconciling apparent contradictions between existing theories.

Preliminary results

I begin by calculating the distribution of community size in the basic model. Since all individuals have equal rates of birth, death and immigration, we can ignore the species identity of individuals for the calculation of community size. If we assume an infinite number of sites and deterministic dynamics, the dynamics of the proportion of occupied sites is given by:

$$(3) \qquad \frac{dP}{dt} = cP(1-P) - eP + i(1-P)$$

where P is the proportion of occupied sites, and c, e and i are the rates of birth, death and immigration, respectively. The first term describes an increase in occupied sites due to local reproduction and depends on both the proportion of occupied sites (affecting the amount of locally produced offspring) and the proportion of available sites (affecting the likelihood of their establishment). The second term describes a decrease due to mortality and depends only on the proportion of occupied sites. The third term describes an increase due to immigration from the regional species pool, and depends only on the proportion of available sites.

Equation (3) is equal to the dynamics in the model of Levins (Levins 1969, 1970), with an added term for immigration (Hanski 1999, Alonso and McKane 2002). The classic Levins model is a deterministic, spatially implicit model of

metapopulation dynamics, where the landscape is modeled as an infinite collection of patches, each able to support a local population. Patches may have only two states – occupied or empty, and within-patch population dynamics is ignored. Dispersal is assumed to be global, so that any patch is accessible from any other patch. The change in the proportion of occupied patches is given by:

$$(4) \qquad \frac{dP}{dt} = cP(1 - P) - eP$$

where P is the proportion of currently occupied patches, c is the rate at which empty patches are colonized, and e is the rate by which occupied patches go extinct. The equilibrium proportion of occupied patches, $P^* = 1 - e/c$, is globally stable and requires that the colonization rate exceeds the extinction rate. Since any population suffers at least some mortality (i.e., $e > 0$), any positive equilibrium is associated with at least some level (e/c) of unoccupied sites.

Tilman (1994) extended the Levins metapopulation model into a model of multi-species dynamics. In this formulation (see also Hastings 1980, Kondoh 2001) the 'patches' are rescaled into 'sites' that hold at most one individual, the extinction parameter, e, is interpreted as mortality rate, and the colonization parameter, c, is interpreted as reproduction rate. As with the original metapopulation model, any stable equilibrium is associated with some fraction of empty sites, implying that ecological communities are never saturated. This contrasts Hubbell's assumption that ecological communities are *always* saturated, and empty sites never exist. This contradiction is particularly problematic because Levins' paradigm that ecological communities are never saturated is a key element of many current theories in population and community ecology (Levin 1974, Hastings 1980, Tilman 1994, Tilman et al. 1997, Holt 1996).

Equation (3) and the equivalent model of Levins (1969, 1970) describe deterministic dynamics of the number of individuals. For the stochastic model I propose with a finite number of sites, the steady state distribution of community size is determined following Alonso and McKane (2002). In a small enough time interval only one demographic event can take place. The dynamics of the probability of each community size is given by:

$$(5) \qquad \frac{dp(J,t)}{dt} = p(J - 1,t)b_{J-1} + p(J + 1,t)d_{J+1} - p(J,t)[b_J + d_J]$$

where $p(J,t)$ is the probability of the local community having J individuals at time t,

$b_J \equiv W(J+1 \mid J)$ is the transition rate from J to $J+1$ individuals, and $d_J \equiv W(J-1 \mid J)$ is the transition rate from J to $J-1$ individuals. By defining $b_{-1} = d_{A+1} = 0$, equation (5) may be used for all states. The stationary probability distribution $p(J)$ is given by setting $\frac{dp(J,t)}{dt} = 0$:

(6) $\quad p(J+1)d_{J+1} - p(J)b_J = p(J)d_J - p(J-1)b_{J-1}$

This gives:

(7) $\quad p(J) = \frac{b_{J-1}b_{J-2}...b_0}{d_J d_{J-1}...d_1} p(0) \qquad\qquad$ for $J=1,...,A$

By applying the constraint $\sum_{J=0}^{A} p(J) = 1$ we get:

(8) $\quad (p(0))^{-1} = 1 + \sum_{K=1}^{A} \frac{b_{K-1}b_{K-2}...b_0}{d_K d_{K-1}...d_1}$.

In the model I propose, an increase in community size can be caused by local reproduction or immigration, while a decrease is caused by mortality. In a small enough time interval dt, such that only one demographic event can take place during it, the possible events are:

- local reproduction, with probability $c\frac{J}{A}(A-J)dt$

- mortality, with probability $eJdt$

- immigration from the regional pool, with probability $i(A-J)dt$

Putting these together, we get:

(9) $\quad b_J = c\frac{J}{A}(A-J) + i(A-J)$

$\qquad\quad d_J = eJ$

The expressions for the transition rates b and d can be replaced by alternative expressions to incorporate more complex demographic mechanisms and/or additional factors that are known to affect the dynamics of ecological communities.

I now describe an approximation method for obtaining the species abundance distribution and species richness in our model. The approximation method integrates the deterministic model of Levins (1969, 1970) with the analytic solution to Hubbell's

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zero-sum model (McKane et al. 2000, 2004, Vallade and Houchmandzadeh 2003, Volkov et al. 2003). I will later show that the method provides good approximation for the results of the proposed demographic model (Figure 1). I ignore stochasticity in community size and assume an infinite area, and find the proportion of occupied sites in a deterministic version of the model, by obtaining from equation (3) the equilibrium proportion of sites P^* for which $\dfrac{dP^*}{dt} = 0$. I then calculate J^*, the characteristic size of the community, as $J^* \equiv P^* A$. Note that J^* can be a non-integer. I further assume that the equilibrium community, as defined by the Levins model, is undergoing a zero-sum game where each death is immediately replaced by local birth (with probability $1\text{-}m$) or immigration (with probability m). Since m is the probability that a death event will be replaced by an immigrant, its value depends on the ratio between the number of locally produced offspring (given by $c(J^*\text{-}1)$) and the number of immigrants (given by iA) in the pool of potential colonizers. Therefore (Vallade and Houchmandzadeh 2003, Etienne and Alonso 2005, Etienne et al. 2007):

$$(10) \quad m = \frac{iA}{iA + c(J^* - 1)}$$

By setting $J = J^*$ and m as obtained using equation (10), equation (2), represented below, gives the full abundance distribution of species j, given its mainland abundance P_j^{reg} (McKane et al. 2000, 2004, Vallade and Houchmandzadeh 2003, Volkov et al. 2003).

$$(2) \quad P_j^{local}(N) = \binom{J}{N} \frac{B(N + P^\wedge, N^* - N)}{B(P^\wedge, N^* - J)}$$

where $B(a,b) = \Gamma(a)\Gamma(b)/\Gamma(a+b)$, $P^\wedge = \dfrac{m(J-1)}{(1-m)} P_j^{reg}$ and $N^* = \dfrac{J-m}{1-m} - P^\wedge$.

Finally, the steady state number of species in the local community, SR, is determined by summing the probability of each species to be present in the local community:

$$(11) \quad SR = \sum_j (1 - P_j^{local}(0))$$

The above-mentioned approximation method predicts the steady state number and relative abundance of species in an unsaturated, equilibrium community where the total number of individuals is determined by the Levins model, and the relative abundances of individual species are determined by Hubbell's zero-sum game. Figure 1 shows that it provides good approximation for the results of the proposed demographic model. This provides evidence that the model I propose might prove useful in reconciling the apparent contradictions between the models of Hubbell (2001) and of Levins (1969, 1970). The approximation method further suggests a demographic interpretation to the input parameters in Hubbell's model, and as such might provide insights regarding their significance and relation to one another. Preliminary analysis shows that the approximation method fails for small areas and low ratios of reproduction to mortality. I will provide a full analytic solution of the proposed model, and will use the solution (accompanied by results of simulations and approximations when a solution is not found) to obtain the objectives of my research.

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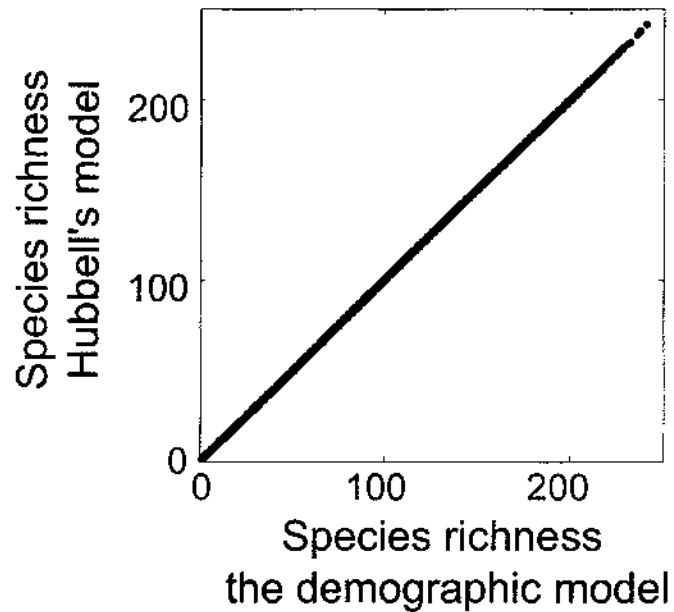
Figures

Figure 1. Correspondence between species richness in the proposed demographic model and in the approximation method. I generated 10000 random sets of the parameters A, c, e and i. For each set of parameters I calculated species richness in the proposed demographic model as described in "the model" section under methods. For each set of parameters I also approximated species richness as described in the preliminary results (equations 2, 3, 9, 10). The 10000 parameter sets were drawn from a uniform distribution in range 0-10000 for A, 0-10 for c, 0-5 for e and 0-1 for i.