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Diversity Patterns from Ecological Models at Dynamical Equilibrium

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We study a dynamic model of ecosystems where an immigration flux assembles the species community and maintains its biodiversity. This framework is particularly relevant for insular ecosystems. Population dynamics is represented either as an individual-based model or as a set of deterministic equations for population abundances. Local extinctions and immigrations balance at a statistically stationary state where biodiversity fluctuates around a constant mean value. We find a number of scaling laws characterizing this stationary state. In particular, the number of species increases as a power law of the immigration rate. With additional assumptions on the immigration flux, we obtain species–area relationships in agreement with observations for archipelagos. We also find power-law distributions for species abundances and lifetimes.

1. Introduction

One of the most interesting statistical relationships in biology is the species–area law, which relates the area of a habitat and the number of species coexisting there. Larger areas harbor more species than smaller ones; this observation goes back to Alexander von Humboldt in the 19th century (see Rosenzweig, 1999). The most commonly used quantitative species–area laws have the form

$$S \propto A^z, \tag{1}$$

(see also He & Legendre, 1996). Such relationships are obtained from the observed species numbers S_i in a number of geographically similar units with areas A_i. Examples are bird species in islands of the same archipelago, plant species in nested sampling areas of a contiguous habitat, or mammals in entire continents (Rosenzweig, 1995).

Thus, these observations cover quite different species and habitat types and extend over a remarkable range of size scales, which points at a universal statistical explanation. The exponent z, of course, is not universal but reflects this diversity. Observed values range from 0.13 to 0.18 for nested areas in the mainland, from 0.25 to 0.33, from 0.5 to 0.8, and from 0.17 to 0.72 for groups of nearby islands, archipelagos, and habitat islands, respectively (Rosenzweig, 1995; Begon *et al.*, 1998). Hence, the growth of diversity is always *sublinear*.

In this paper, we present elements of a scaling theory for ecosystems, which provides a conceptual framework to understand the appearance of species–area relationships. We analyse different dynamical models of co-evolving populations subject to an immigration flux. A number of scaling laws are obtained for ecological quantities of interest, which include the distribution of species lifetimes and biomasses. The number of coexisting species, in particular, is found to be a power of the immigration rate,

$$S \propto I^a. \tag{2}$$

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Here, I is defined as the average number of new species (i.e. species not yet present in the ecosystem) arriving per unit of time. The exponent takes values typically in a narrow range, $0.4 < a \leqslant 1$, depending on the system parameters. With reasonable assumptions on the area dependence of the immigration flux, this translates indeed into species–area laws of the form (1). The latter thus appear important but are not the only manifestations of scaling in ecosystems.

In this model, biodiversity is established and maintained by a constant average flux of immigrating species. At long times, the system always evolves to a *stationary state* where immigrations and local extinctions balance. This stationary state is characterized by a continuous turnover of species and time independent distributions for ecological variables like the number of species, the number of trophic levels, the number of links per species, or the species abundances. The scaling laws (1) and (2) refer to the average values of species number and immigration flux. The actual time series for a given ecosystem, $S(t)$ and $I(t)$, fluctuate around the averages, and these fluctuations are determined by the stationary distributions. We emphasize that the stationary state is *strongly driven*: It depends on a non-zero immigration flux and, hence, it cannot be described by a fixed point of population dynamics.

This *dynamical* view of ecosystems goes back to the seminal work of MacArthur & Wilson (1963). Their theory of island biogeography explains the number of species as given by a dynamical balance between the arrival of new species (immigration) and local extinction. The resulting stationary state has been called a *dynamical equilibrium*. Many field studies and statistical analysis of data have tested this theory. They range from island defaunation experiments (Simberloff & Wilson, 1969) and subsequent analysis (Simberloff, 1969; Heatwole & Levins, 1972) to the study of insular biodiversity patterns (Gilpin & Diamond, 1976) and of fluctuations of the number of species (Gilpin & Diamond, 1980, 1981; Manne *et al*., 1998). On the theoretical side, the lack of explanatory power of MacArthur and Wilson's theory has been criticized (Williamson, 1989; Whittaker, 1992), and corrections have been proposed (Simberloff, 1969). In our view, its major shortcoming is the lack of a foundation on population dynamics.

The dynamical view should be contrasted with the *static* picture of ecosystems as stable fixed points of population dynamics. A famous result for static networks is May's theorem (1972): An ecosystem of $S \gg 1$ species connected randomly by C links whose strengths are drawn from a distribution with average 0 and variance σ^2 will have (with probability 1) no stable fixed point if $\sigma^2 CS > 1$. This result, which has been slightly corrected later (Cohen & Newman, 1985), sets an upper limit to the amount of complexity allowed by the stability condition. Clearly, the static picture is not appropriate to describe ecosystems with a continuous turnover of species. May's theorem does not apply to these networks since the links between species are not random variables but are themselves subject to selection. Indeed, the species number found in our model systems are often much larger than that expected from May's theorem.

A number of authors obtain species area relationships from models without explicit population dynamics. Preston (1962) derived a power-law relationship from the assumption that the abundance of species is characterized by a log–normal distribution. This assumption has been questioned, however, since field studies support broader distributions. Harte *et al*. (1999) obtained a species–area relationship of the form (1) from a self-similarity hypothesis for the spatial distribution of individuals. Their model thus applies to nested areas, however, the assumption of self-similarity lacks a dynamical justification to date. An analytical relation between the spatial distribution and the species distribution was subsequently derived (Banavar *et al*., 1999). Several recent models try to include immigration or speciation in an effective way, still without explicit population dynamics. Wissel (1992) modeled an ecosystem of similar species, combining the effects of environmental and demographic stochasticity with interspecies competition. Durrett & Levin (1996) proposed a model where speciation is coupled to contact dynamics to mimic ecological processes, and obtained nearly power law species area relationships. Loreau & Moquet (1999) modeled immigrations of plant species from a large pool to an island, including

explicit competition for space. A recent model for species turnover has reproduced power-law distributions for species abundances and species lifetimes as observed in field studies (Solé *et al*., 2000).

Recent studies based on explicit population dynamics include Pelletier (1999), who coupled a diffusion mechanism to spatial noise and obtained a power law species area relationship. In this model, however, there is no explicit interaction among species. Caldarelli *et al.* (1998) and Drossel *et al.* (2001) coupled population dynamics to speciation and obtained food webs with a broad distribution of biodiversity. Another class of models which combine immigrations and population dynamics is that of species assembly (Post & Pimm, 1983; Drake, 1990; Case, 1990; Morton & Law, 1997; Happel & Stadler, 1998; Schreiber & Gutierrez, 1998). In these models, a community is constructed through local immigrations from a regional species pool. After every immigration, the new community is tested for persistence (i.e. the property that no species gets extinct even in the limit of infinite time). Imposing the condition of persistence limits these models to the regime of rare immigrations, while in our approach the immigration rate is an independent parameter.

It is clear that any consistent theory for long-term co-evolution cannot be based on population dynamics alone. It has to include processes that create new species and modify the trophic links of the network. These processes are adaptive mutations, speciations, and immigrations. As discussed above, they act as driving forces that prevent the system from settling at a stable fixed point of population dynamics. Here, we focus on the case where immigration is the dominant process, which may be most appropriate for relatively small insular ecosystems receiving a flux of species arriving from a larger 'continental' pool. Networks where speciations and mutations are relevant driving forces as well are discussed in separate papers (Lässig *et al*., 2001; Bastolla *et al*., in preparation).

Since this model has no spatial structure, it is applicable only to cases where spatial heterogeneities (e.g. in the population densities) can be neglected. This is clearly a more reasonable assumption for isolated islands (or entire archipelagos) than for groups of islands or nested continental areas, where migration fluxes between the single units become important. It is tempting to speculate, of course, that the dynamical mechanism described here is generic.

Immigration-driven systems have two important time scales: the relaxation time τ of population dynamics and the average time between immigrations, $1/I$. The former depends on the size and the interactions of the network, the latter is taken here as an independent parameter. Their ratio turns out to determine the scaling properties of the ecosystem. If immigrations are rare ($\tau I \ll 1$), the population dynamics gets close to stable fixed points in between. The immigrant species are merely a sequence of potential invaders of these stable communities; the ecological properties of these slowly driven networks are asymptotically independent of the immigration rate. In the opposite limit ($\tau I \gg 1$), immigrations are so frequent that they essentially randomize the species network. At intermediate immigration rates, both immigrations and ecological dynamics play an important role, and the stationary state depends on I in a non-trivial way. This is exemplified by the power law (2) of the species number as well as by other characteristics of the ecosystem. The number of trophic levels increases with I, consistently with the observation that food chain length is positively correlated to the size of the ecosystem (Schoener, 1989) and with a recent simulation (Spencer, 1997). The distribution of species abundances has a power-law shape, with an exponent close to -1 and slowly decreasing with the immigration rate. The first result is in agreement with field observations (Pielou, 1969), considerations based on the theory of multiplicative processes (Kerner, 1957; Sornette, 1998; Biham *et al*., 1998) and analytic results from a similar model (Solé *et al*., 2000), and seems to be rather general. The distribution of species lifetimes has also, in an intermediate range, almost power-law shape, with an exponent close to -2, and slowly decreasing with the immigration rate, as expected. This result is also in agreement with field observations (Keitt & Marquet, 1996; Keitt & Stanley, 1998) and with the results of Solé *et al.* (2000).

It would be of course interesting to compare eqn (2) directly to observations, but one would need a set of islands of comparable area and geographical location and varying distance from the continent. Thus, in order to compare eqn. (2) to observed species–area laws, we have to assume a functional relationship between immigration rate and area. First, we assume that I is proportional to the square root of the area: for instance, it can be proportional to the diameter of the island seen from the continent (MacArthur & Wilson, 1963). This case is relevant for situations where there is a unique source of immigrants. Remarkably, we then obtain eqn (1) with an effective exponent around 0.5, in good agreement with the value observed for entire archipelagos or isolated islands. Second, with an immigration rate independent of area, we obtain a logarithmic species–area relationship, $S \propto \log(A)$, in agreement with observations for the central cluster of Salomon islands. In this case, the connectivity of an island plays indeed a bigger role than its area in determining the immigration rate. In intermediate situations, the species–area law obtainable from our model should lie between these two behaviors. It is tempting to speculate that different exponents of the species area relationship observed for different groups of nearby islands, and usually smaller than 0.5, could reflect mainly different relationships between immigration rate and area.

This paper is organized as follows. Section 2 contains the stochastic Individual Based Model of ecological dynamics. The alternative formulation of this dynamics as a deterministic Lotka–Volterra system follows in Section 3. The results for both cases are presented together in Section 4 and related to the framework of MacArthur and Wilson's phenomenological theory in Section 5. The paper concludes with a discussion.

2. An Individual Based Model

Recently, population ecology has started to use individual-based (or individual-oriented) models (IBM) as a complementary tool in the study of ecological dynamics (Lomnicki, 1999; Grimm *et al*., 1999). One of the main interests of such an approach is that it allows the explicit modeling of individual characteristics, like the age of the individuals in a population (influencing the time of breeding or the moment at which they die), or the energy that they store and require to move and survive (Bascompte *et al*., 1997). Most IBM studies refer to concrete problems where a few species of known characteristics interact to produce a well-defined behavior or pattern, which the IBM should recover or predict (Fahse *et al*., 1998; Spencer, 1997). Another interest of IBM is in what has been termed *virtual ecology*: The comparison between real data and simulated data obtained from a system where realistic restrictions have been considered might allow the design of better protocols for recruitment and observation (Berger *et al*., 1999; Hall & Halle, 1999).

Simulations of very large systems with many individuals and/or many species have not been undertaken until recently because of computational limitations. Thus, the IBM approach was restricted to few species in relatively small lattices representing real space, with one to few individuals per lattice site. More ambitious problems, like the relation between theoretical results for deterministic continuous models and their IBM counterpart, were addressed only recently (Keitt, 1997). Some authors derived time-continuous models from the more basic description of the flow of energy between constituents (Svirezhev, 1997) or among individuals (Wilson, 1998; Solé *et al*., 1999). This is indeed a very relevant point. One would expect that the coarse-grained higher-level description represented by deterministic models captures the essential features of lower-level individual-based models. This is in fact the philosophy behind our approach: In the IBM, as well as in the higher-level models to be introduced in the forthcoming sections, we study the predictions of the model from a statistical point of view, ignoring details that will necessarily be different in different models.

2.1. ECOLOGICAL DYNAMICS

Consider a large area A_{cont} on which a maximum number M_h of basal species coexist and up to M_a animal species compete for resources. The ecological interactions in this community will be

defined through a matrix with entries $C(m_i, m_j)$. Depending on the values of $C(m_i, m_j)$ and $C(m_j, m_i)$ we will determine the trophic relationship between individual i of species m_i and individual j of species m_j, as we explain later. We have considered two possible algorithms to determine the non-zero elements of the interaction matrix. Our first election corresponds to the cascade model (Cohen *et al.*, 1990), which returns a network with topological properties comparable to those of real ecosystems. In this case, the distinction between basal and animal species automatically arises from the ecological relationships given by the interaction matrix. We define $M = M_h + M_a$ to be the total number of species in the system. If the number $m_i = 1, \ldots, M$ specifies a pecking order for feeding, the algorithm works as follows: Any species m_i can feed only on species m_j which is lower in the order, that is, $m_j < m_i$. This avoids the formation of loops. A link to any of the potential prey species is established with probability ℓ/M. If the value of ℓ is fixed (according to real observations) to be around four, this model returns the correct proportions of basal, intermediate, and top species, a maximum number of levels typically around ten, and a distribution of the number of predators per prey which agrees with field observations (Cohen *et al.*, 1990).

A second possibility for the interaction matrix consists in randomly assigning ℓ preys to each of the M_a animal species. This would correspond to a disordered situation where no processes have acted in order to select the topology of the ecological network. In this case, and only for implementation purposes, basal species occupy positions $m_i = 1, \ldots, M_h$, and animal species occupy $m_i = M_h + 1, \ldots, (M_h + M_a)$. The interaction matrix has the form

$$\left(\begin{array}{c|c} 0 & 0 \\ \hline C(m_a, m_h) & C(m_a, m_a) \end{array}\right),$$

where m_h and m_a indicate basal species and animals, respectively. The statistical properties of the system do not depend on the topology of the interaction matrix. As we will see, the relevant quantities take the same form in the cascade model case (CM) and in the random matrix case (RM). For both algorithms, the values of the matrix elements are randomly chosen from a uniform distribution in $[0, E]$, where $E \in [20, 200]$ (see Table 1). The value of the matrix coefficients is proportional to the energy gained by individual i when feeding on individual j and represents a sort of assimilation efficiency (see below).

TABLE 1
Parameters in the individual based model

p_d	Death probability
d	Dissipation rate
N_h	Max. Ind. in basal species ($\simeq$ island area)
$B(> d)$	Basal growth
$C(m_i, m_j) \in [0, E]$	Energy obtained by i when eating j
$E_{rep} \simeq 2E$	Reproduction energy
δ	Energy when born
$\ell = 3, 4$	Number of preys per predator
M_h	Max. number of basal species
M_a	Max. number of animal species
I_0	Bare immigration rate

In determining the matrix C, we have essentially defined a structured ecosystem in a very large area with many species. This is what we consider to be the continent, which will be the source of immigration of propagules to an island of area N_h. This last quantity can be understood as the maximum number of patches covered by grass, for instance, and acts as a main limiting value (together with the basal growth, to be defined) for the number of animals that will inhabit the island.

At time t, and once we properly define the immigration mechanism, we will have a number $n_h(t)$ of individuals in basal species present on the island and a number $n_a(t)$ of individuals belonging to animal species. The total number of individuals in a wide sense (say patches of grass plus animals) is $n(t) = n_h(t) + n_a(t)$. Each individual is characterized by an energy $e(i)$. Individuals reproduce provided their value of $e(i)$ is large enough. Basal species increase their energy at a constant rate. Animals dissipate energy as time elapses, and increase the value of $e(i)$ through predation, which happens stochastically. At each time step the following rules are implemented:

1. *Pair formation.* At each time step, we randomly form $n(t)/2$ pairs of individuals, independently of their specific affiliation. If $n(t)$ is odd,

one individual remains without partner. Different possibilities are (i) *h–h* pair: the two grass patches are not consumed by animals and keep their energy, (ii) *a–h* pair: if the matrix element $C(m_a, m_h)$ is positive (meaning that the individual *a* feeds on *h*), predation is possible, (iii) *a–a* pair, allowing predation between different animal species depending on the matrix coefficients.*

2. *Predation and Feeding.* Either of the individuals in each pair (i, j) can feed on its partner, according to the ecological relations defined in the matrix $C(m_i, m_j)$. Predation happens when $C(m_i, m_j) \neq 0$ and $C(m_j, m_i) = 0$. In this case,

$$e(i) \to e(i) + C(m_i, m_j) \times \frac{e(j)}{E_{rep}},$$

$$e(j) \to 0,$$

where E_{rep} is an energy scale related to reproduction, that will be defined below. The energy received is proportional to the matrix element, but also to the energy stored in the predated individual. In this sense, to eat a new born is not equivalent to eating an adult close to its reproductive energy (which fixes the maximum energy). Furthermore, an individual cannot increase its energy beyond $E + E_{rep}$. In addition, if the value of the fraction $e(j)/E_{rep}$ is larger than unity the rule is modified as $e(i) \to e(i) + C(m_i, m_j)$.

If both $C(m_i, m_j)$ and $C(m_j, m_i)$ are non-zero (or both zero), no interaction takes place.

3. *Basal growth.* Every individual belonging to a basal species increases its energy at each time step by a net amount *B*,

$$e(i) \to e(i) + B \quad \text{if } m_i \in [1, M_h].$$

4. *Dissipation.* At each time step, and for each of the animals alive, $e(i) \to e(i) - d$, where *d* defines the dissipation rate. It takes the same value for all species in our model.
5. *Reproduction.* If $e(i) \geqslant E_{rep}$, the individual *i* is allowed to reproduce. In the case of basal species, the new individual is introduced into the system provided there is place, i.e. if $n_h(t) < N_h$. The individual which reproduces loses an amount of energy δ,

$$e(i) \to e(i) - \delta,$$

$$e(k) \to \delta,$$

where $e(k)$ is the energy of the new born.

6. *Death.* An individual can die for three different reasons: If its energy reaches zero, if it is eaten by a predator, and with a fixed probability p_d per time step.

Table 1 resumes the parameters of the model and the range of values used in our simulations. We will present results for some representative cases. No qualitative differences were observed for comparable sets of parameters.

2.2. MODELING IMMIGRATIONS

We can think of the initial matrix $C(m_i, m_j)$ as representing predator–prey relationships among a pool of species in the continent, where a very large area (with its resources) allows the coexistence of all possible species (in our case $M = M_h + M_a$). An island has a finite area N_h and harbors only a subset M_{isl} of M.

The immigration flux I_0 represents the number of individuals arriving from the continent to the island, and can take values from the set $\{\ldots 1/4, 1/3, 1/2, 1, 2, 3, \ldots\}$ only. If $I_0 = q \geqslant 1$, then q new individuals randomly chosen from any of the possible M species in the pool arrive at the island, at each time step. If $I_0 = 1/q < 1$, one individual is introduced every q time steps. Other situations, which imply a less smooth flux, are excluded in the following. This *bare* immigration flux is independent of the specific composition of

*This rule can be understood as a rough picture of a space-explicit aproach since, although there is no representation of the physical position of an individual, the interaction among species is neither global nor simultaneous. For example, if a species and its feeding source both occur at low densities, the probability for that species to survive is small mainly due to stochastic effects: It takes some time to "find" the prey, as would happen with a blind search in real space. In this sense, the random pair formation is suboptimal when compared to global deterministic interaction (see below), and closer to an explicit space formulation. Actually, for $n_h(t) > n_a(t)/2$, this pair formation is indistinguishable from the real space formulation in which animals can occupy a randomly chosen site at each time step (uncorrelated movement).

the system. On the other hand, the probability that a species is new on the island or is accepted in the community does depend on the set of established species. When the simulation starts, basal species have a higher probability of colonizing, while animal species can become persistent only when the former are already established. The flux of *new* immigrants (the net flux) varies in time, as observed in real situations.† For moderate to large I_0 (there are enough proposals for new species, many different individuals try to colonize the island), the observed ecosystem is shaped through ecological interactions. In this regime, the introduction of differential immigration rates does not produce qualitative changes in the ecosystem properties.

Our simulations show that the average number of species coexisting on the island depends very strongly on the vertical transmission of resources, as is well known to happen in real ecosystems (Rosenzweig, 1995). High dissipation relative to basal growth (d close to B) turns into a few species on the island. For $d \ll B$ (a factor of 2 or 3 may suffice) the average number of species coexisting when I_0 is large enough approaches the maximum number M.

With the addition of a constant flux of species from the continent to the island, the system is poised to a state of dynamical equilibrium, where the number of species that disappear due to the ecological interactions or to demographic stochasticity is balanced by the new incoming species. The immigration rate might produce a rescue effect for species with few individuals, close to extinction, and at the same time includes in a natural way one form of environmental stochasticity.

Thus, the incoming flux of individuals from the continent, the immigration rate, becomes our main variable. By changing its intensity, we can calculate the average number of species S present in the statistically stable regime on an area $A \equiv N_h$. Moreover, assuming a relation between the immigration rate I_0 and the area A, we will derive the species–area law resulting from the ecological dynamics of the IBM and compare it with field data.

†In the next section we will use the net flux I instead of I_0 to characterize immigration. In Section 5 we relate both quantities by taking into account the species present on the island.

3. Deterministic Continuous Model

In this section, we present the deterministic continuous models of population dynamics adopted in our simulations. All individuals belonging to a species are grouped together and represented through a single dynamic variable, the density of biomass (or abundance) of species i at time t, $N_i(t)$. In contrast to the IBM, where interaction among individuals was stochastic, here it is deterministic.

3.1. ECOLOGICAL DYNAMICS

The population densities of the species $i = 1, \ldots, S$ evolve through a system of differential equations,

$$\frac{\mathrm{d}N_i}{\mathrm{d}t} = -\alpha_i N_i(t) - \beta_i N_i^2(t) + \sum_j g_{ij}(\{N_k\}) N_i(t), \tag{3}$$

which determine the growth rate of the biomasses as a function of the abundances of all other species in the ecosystem. Species with biomass less than a pre-defined threshold value N_c become extinct and are eliminated from the system. This mimics the effect of demographic stochasticity and the fact that species are made of discrete entities.

The first term on the r.h.s. of eqn (3) stands for the dissipation of energy following the biological activity of the members of species i (movement, extraction of nutrients, basal metabolism), as well as the death rate of individuals. The coefficient α_i corresponds to the quantities d and p_d of the IBM. The term $-\beta_i N_i^2(t)$ is known as self-damping. It expresses a negative feedback of N_i on its own growth rate, which in some instances is required for stability. The terms $g_{ij}(\{N_k\})$ are the *predator functional response* (PFR) to prey j, and represent the biomass transferred per unit time from species j to species i if the sign is positive, and from species i to species j if it is negative. They model prey–predator interactions and correspond to the matrix $C(m_i, m_j)$ in the IBM.

Energy flows into the system through the coupling of basal species to external resources, which are formally represented as an additional "species" N_0 whose equation will be specified below. Terms of the form g_{i0} are thus equivalent to the parameter B in the IBM. However modeled, external resources introduce in the system an energy scale R which limits its total biomass.

We studied two different variants of the continuous model, with different functional responses and different equations for the resources.

- Model A: Prey-dependent functional response and biotic resources.

  The predator's functional response belongs to the category of *prey-dependent* functional responses, and is proportional to prey's biomass, $g_{ij}(\{N_k\}) = \gamma_{ij} N_j$. The coefficients γ_{ij} take values in the interval $\gamma_{ij} \in [0, \gamma_{max}]$.

  In order to represent competition among basal species, we introduce a fictitious dynamics for the resources $N_0(t)$ (thus biotic resources), modeling them through an equation of the same kind as eqn (3),

$$\frac{1}{N_0}\frac{\mathrm{d}N_0}{\mathrm{d}t} = \gamma_0 R + \sum_j \gamma_{0j} N_j. \tag{4}$$

  The constants γ_{0j} have all negative signs and we assume that at least one basal species is present.

  In Lotka–Volterra equations with prey-dependent functional response, the quantity α/γ_{max} introduces an energy scale in the ecosystem, besides the other energy scales R, N_c and α/β. One can expect different regimes for different relative values of these energy scales, and this is indeed what we observe. Not all these regimes are biologically meaningful. For instance, for small values of the dimensionless parameter $u = \gamma_{max} N_c/\alpha$ dissipation effects dominate and only basal species can survive in the long run. This *garden regime* is briefly described in Appendix A.

- Model B: Ratio-dependent functional response and abiotic resources.

  The additional energy scale introduced in Model (A) through the parameters α/γ_{max} is not present in *ratio-dependent* PFR (Arditi & Ginzburg, 1989). In this case, the PFR g_{ij} depends on the ratio between the prey biomass and the predator biomass. When the prey j has a unique predator i the functional response is given by

$$g_{ij}(\{N_k\}) = \frac{bcN_j}{bN_j + cN_i}. \tag{5}$$

  In the case of several predators for the prey j, different generalizations of eqn (5) have been proposed (Arditi & Michalski, 1995; Schreiber & Gutierrez, 1998; Drossel *et al.*, 2000). We adopt our own PFR, which reads

$$g_{ij}(N_k) = \frac{b_j c_{ij} N_j}{b_j N_j + \sum_{k\in P(j)} c_{kj} N_k}, \tag{6}$$

  and where i is the predator and j the prey; b_j is a rate coefficient, and c_{ij} stands for the rate at which a single individual of species i, in the absence of competition, consumes a corresponding quantity of biomass from species j. The sum is performed over the set $P(j)$ of predators of j, among which i is included.

  The above equations, unlike model (A), explicitly represent the competition among predators of the same prey. It is then possible to model external resources as a constant flux of energy available to basal species,

$$N_0(t) \equiv R. \tag{7}$$

Ratio dependent and prey dependent functional responses have been supported and criticized in several papers [see Abrams & Ginzburg (2000) for a recent review]. We do not want to enter into such a debate here. Any functional response is just a crude representation of a much more complicated situation, in which spatial distributions of individuals, foraging strategies and mating behavior are involved. The point raised in this paper is that, although model (A) and model (B) may have different scaling properties, the scaling behavior of biodiversity is robust with respect to changes in the functional response, in an appropriate range of parameters. Indeed, we observe that model (B) gives results qualitatively similar to those of model (A) for

intermediate values of $u = \gamma_{max} N_c/\alpha$. In this range, and for both models, S scales as $\log(R/N_c)$.

3.2. IMMIGRATION AND ECOLOGICAL PARAMETERS

At time $t = 0$ no species is present on the island. New species arrive one after another, at fixed intervals of time, $1/I$. Between successive arrivals, population dynamics equations are integrated and species may die out.

For every new species, the ecological parameters are chosen at random and kept fixed until the species become extinct. This means that new species are not related to species already on the island, that is, the continental pool is considered infinite with respect to the number of species on the island. Additionally, this allows to disentangle finite size effects due to a limited number of species in the pool from the role played solely by the immigration rate.

New species have no predators on the island and a number ℓ of preys is randomly extracted between one and ℓ_{max} (in most simulations we used either $\ell_{max} = 4$ or $\ell_{max} = 8$). The ℓ preys are extracted with uniform probability among the $S(t)$ existing species, regarding the external resources N_0 as a normal prey. This operation defines the ecological network. Here, the specific composition of the bare immigration flux changes in time (this does not happen in the IBM), since the probability that the new species is a basal species (linked to the resources) decreases with an increasing number of species on the island. In the stationary state, it becomes constant on the average. As we will see, the statistical properties of the ecosystem are robust with respect to these changes in the immigration rules.

For every link, the interaction strengths γ_{ij} are extracted from a uniform distribution in $[0, \gamma_{max}]$ in the case of model (A). In the case of model (B), the parameters c_{ij} are extracted uniformly in $[0, c_{max}]$, and $b_j \equiv 1$. In both cases, i is the predator and j is the prey, and we then make the assumption that the interaction strengths are antisymmetric: $g_{ji} = -g_{ij}$. We also studied the case of reduced efficiency, $\gamma_{ij} = -\eta\gamma_{ji}$, with i predator, j prey and $0.5 < \eta < 1$, without observing any qualitative difference. In case of model (A), the parameter γ_0, proportional to the growth rate of the resources N_0, is set to $\gamma_0 = \gamma_{max}$. As a simplification, the dissipation parameters are the same for all species $\alpha_i = \alpha$, $\beta_i = \beta$.

Colonizing species arrive with very small populations $N_{max} = N_c$. This assures that they are rapidly eliminated if they do not have preys on the island. Increasing the initial size increases spurious effects due to species with very short permanence in the system, and has only a very small influence on the statistical patterns described later.

3.3. DISCUSSION OF THE MODELING CHOICES

The choice that new species have preys but not predators on the island has to be justified. From a practical point of view, this rule forbids the formation of ecological loops. Moreover, newcomers now have considerable chances of surviving. Note that in the IBM, and since new species might not find an available feeding source, the rate of arrival of species with non-vanishing permanence time presents fluctuations larger than in this case, hence increasing the fluctuations of all ecological variables. With the rule now implemented, the resulting ecological networks very much resemble those obtained with the application of the cascade algorithm (used in the IBM model). Despite these differences in the modeling of immigration, the statistical behavior of the system is not strongly dependent on the different choices: finite pool with random interactions or cascade model (IBM) or infinite pool with cascade model (continuous models). The different descriptions adopted amount to a simple rescaling of the immigration rate I. For example, relaxing the rule that a new species only has preys on the island would decrease its chances of being accepted. A similar acceptance rate would nevertheless be obtained for a larger value of I.

Our simulations considered several representations of the ecological dynamics at the individual and at the population level. Although our consistent results let us believe that the models capture generic properties of ecological networks, there are a number of alternative (and equally plausible) dynamical rules or generalizations of our rules that would be interesting to consider. We shortly discuss some of them.

First, fixing the ecological quantities α_i and β_i equal for all species is quite unbiological. On the other hand, extracting random values of α_i and β_i for each species would lead the average value of these parameters to decrease towards zero, due to the advantage conferred by small dissipation rates and self-damping. In order to avoid this effect, we believe that it is necessary to model a trade-off between dissipation, α_i, and predation efficiency (γ_{ij} or c_{ij}), in such a way that the latter is an increasing function of the former. Another critical point is that all pairs of coefficients g_{ij} and g_{ji} have, in our model, opposite signs, so that symbiotic relationships are not represented.

Regarding the network structure, it is certainly a significant simplification to build links independent of each other. For a more realistic model, one needs a measure of the distance among species in some multidimensional space. It would then be possible, for instance, to extract at random the first prey of a new species, and then to extract the remaining preys with a probability depending on the distance from the first prey. Regarding the topology of the network of interactions, it is comforting that ecological networks constructed using both the cascade model and random matrices containing loops (in two different dynamical frameworks) returned the same qualitative behavior.

For a very long time, co-evolution of species would become relevant. This might be taken into account by making appropriate modifications in the ecological network or in the interaction parameters. Discarding coevolution is justified if the time scale of the simulation is much shorter than the time after which at least one species in the ecosystem mutates. Nevertheless, the latter time scale is expected to decrease as the number $S(t)$ of species in the ecosystem increases, until a point where it is not possible anymore to neglect coevolution. Such a situation is worth considering and will be the subject of future work.

4. Statistical Features of the Stationary State

For every set of observations, we present both results obtained with the continuous model and the IBM, whenever available. In fact, the two descriptions produce the same qualitative behavior, even if simulations are much faster for the continuous model, so that it is possible to simulate larger systems and to obtain better statistics.

When we extract at random an ecological network with a high number of species (up to 1000) and a low number of links per species (for instance four), the ecological dynamics leads to the extinction of most of the species, until only very few are represented in the system. This result does not seem to depend on the way in which the links have been extracted (either using random matrices or through the cascade model), on the parameter values, or on the kind of ecological dynamics represented (individual based or continuous, with prey dependent or ratio dependent PFR).

In the presence of a constant flux of immigrant species, the ecosystem, initially empty, grows very fast in diversity until it reaches a number of species which remains on the average stationary in time, although characterized by relatively large fluctuations. This process is illustrated in Fig. 1. The system differs significantly from a static network: In fact, if we stop immigrations we notice an abrupt decrease in the number of species until a fixed point of much lower diversity is reached (see Fig. 1).

Choosing as time unity the quantity $1/\alpha$ and as biomass unity the external resources R, the dynamical equations can be written in terms of four dimensionless parameters. For model (A) they are:

$$\gamma'_{max} = \gamma_{max} R/\alpha, \; N'_c = N_c/R,$$
$$\beta' = \beta R/\alpha, \; I' = I/\alpha, \tag{8}$$

while for model (B) the first parameter is substituted by

$$c'_{max} = c_{max}/\alpha. \tag{9}$$

Together with the maximal number of preys for a colonizing species ℓ_{max} these parameters determine the model ecosystem. An overview of the parameters characterizing models (A) and (B) is presented in Tables 2 and 3.

We observe a turnover of species in the system, and even a complete change in the species

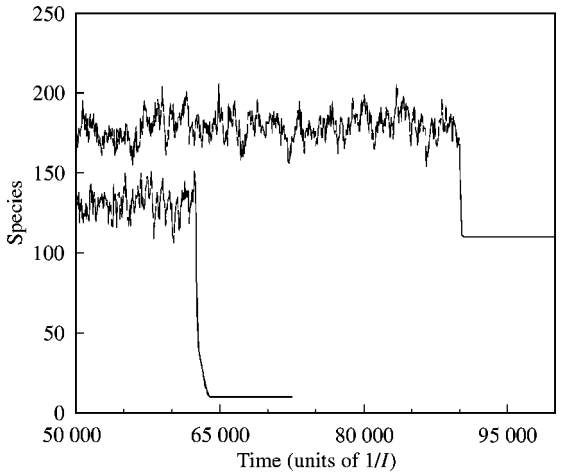

FIG. 1. Number of species as a function of time in two typical realizations of the continuous model. The upper curve was obtained with eqn (3) using the following parameters: $N_c' = 10^{-3}$, $\beta' = 10^4$, $\gamma'_{max} = 5000$, $\ell_{max} = 8$, $1/I' = 7 \times 10^{-4}$. The lower curve was obtained with model (B) and parameters $N_c' = 10^{-4}$, $\beta' = 10$, $c'_{max} = 20$, $\ell_{max} = 8$, $1/I' = 7 \times 10^{-3}$ (see Tables 2 and 3). In both cases, only the final part of the evolution is shown. After a fast transient ($t < 1000$), the system reaches a dynamical equilibrium state. The steep decrease of biodiversity corresponds to stopping the immigration rate. This last part and the initial transient part of the curves were not used to measure stationary quantities.

TABLE 2
Parameters common to the continuous models (A) and (B)

α	Dissipation of energy and death rate
β	Self-damping
$g_{ij}(\{N_k\})$	Predator functional response
N_c	Extinction threshold
R	Abiotic resources
I	Net immigration rate
ℓ_{max}	Maximum number of prey for immigrant species
N_{ini}	Initial population of an immigrant species

Dimensionless parameters

$\beta' = \beta R/N_c$ $\quad N_c' = R/N_c$ $\quad I' = I/\alpha$

composition of the island in the course of time. In the IBM model, where we use a fixed continental pool of species, the presence of different basal species determines the intermediate and top species allowed by the subnetwork on the island. Due to stochastic effects, we observe a turnover of basal species (often after a long time interval),

TABLE 3
Parameters characteristic of each continuous model

Model A: Prey dependent PFR and biotic resources

$\gamma_{ij} \in [0, \gamma_{max}]$	Interspecific interaction
$\gamma_0 = \gamma_{max}$	Biotic resources growth rate

Dimensionless parameter: $\gamma'_{max} = \gamma_{max} R/\alpha$

Model B: Ratio dependent PFR and abiotic resources

$c_{ij} \in [0, c_{max}]$	Consumption rate of j by i
$b_j \equiv 1$	Rate coefficient

Dimensionless parameter: $c'_{max} = c'_{max}/\alpha$

and consequently a complete renewal of the island ecosystem (see Fig. 2). This picture agrees qualitatively with experiments on island repopulation (Simberloff & Wilson, 1969; Heatwole & Levins, 1972; Simberloff, 1969), where, after defaunation, a different specific composition was obtained.

4.1. SPECIES DIVERSITY AND RELATION AMONG TIME SCALES

When the stationary state is reached, we observe that, for some range of parameters, the average number of species S increases as a power law of the immigration rate I,

$$S \approx S_0 + cI^a, \tag{10}$$

with a constant S_0 usually very small (its value is particularly sensitive to the parameter β). Note that if I would be strictly zero, then our system would be empty. But in the limit of arbitrarily small (yet positive) values of I a finite number of species (S_0) can persist in the island, as long as their characteristic permanence time is larger than $1/I$. This limit corresponds to the fixed point of the dynamical equations for the network.

We define a new exponent b, that we call competition exponent, as

$$b = \frac{1}{a} - 1. \tag{11}$$

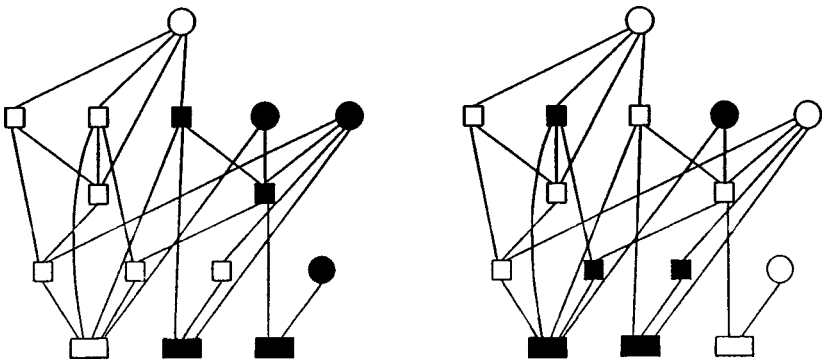

FIG. 2. Two different ecological subnetworks for the IBM model observed on the island for the same network in the continent. The specific composition might be different at different time moments as a result of the turnover of species and of the alternating dominance of different basal species. Here we show the result of a simulation of a small "continent" with a total number of 15 species. Within an interval of 3000 time steps, the two configurations represented by filled symbols (for species actually present on the island), were observed. Circles stand for top species, squares for intermediate, and rectangles for basal ones.

In the stationary state, the average extinction rate per species is $e = I/S$ and increases with the number of species at equilibrium as S^b (for $S \gg S_0$), whence the name of competition exponent,

$$e \propto S^b. \tag{12}$$

Since the exponent b is larger than zero, the larger the number of species, the smaller the time scale for the extinction of a single species. The fact that the extinction rate increases with the number of species has been postulated in the theory of island biogeography. However, we find this result not as a phenomenological law, but as a generic feature of the dynamics of randomly assembled networks subject to ecological dynamics. We first present results from the IBM and then compare them with those from the continuous models, eqn (3).

The results of the IBM model are summarized in Fig. 3. Four curves displaying the average number of species S as a function of the immigration rate I are plotted. Curves qualitatively similar to ours were obtained in other simple models for island colonization (Rosenzweig, 1995; Loreau & Mouquet, 1999), but the functional relationship between I and S was not investigated.

All curves in Fig. 3 show two plateaus corresponding to a (i) low diversity regime (small immigration rate), and (ii) disordered species composition (large immigration rate), which are linked by a transition region with power-law

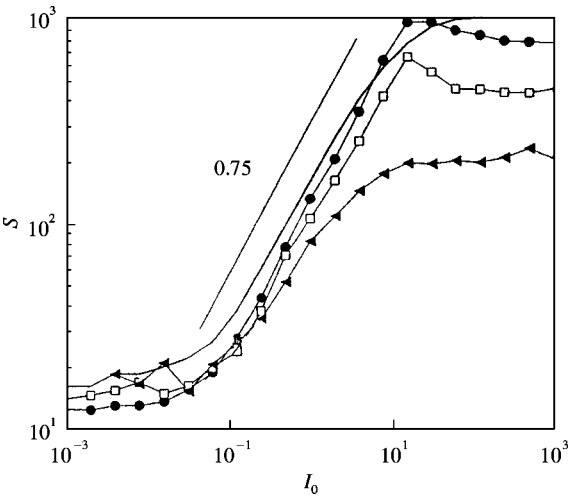

FIG. 3. Average number of species at stationarity in the IBM model as a function of the immigration rate I_0. Three different regimes are observed as I_0 is increased. The parameters for each of the curves are: $N_h = 10^4$, $M_h = 100$, $M_a = 900$, $E = 100$, $E_{rep} = 200$, $\ell = 3$, $b = 5$, $d = 2$, $\delta = 20$, $p_d = 0.002$ (▲—▲); empty squares correspond to the same parameters with $d = 1$, and solid circles to the same situation but $E = 150$, $b = 10$, and $d = 1$. These three curves have been obtained from random interaction matrices (RM). The solid line corresponds to a simulation of the CM with parameters as in the last case.

shape described by eqn (10). The effective exponent obtained from a power-law fit is $a \simeq 0.75$. This intermediate regime is the most interesting one, since here both the immigration rate and the ecological organization play a relevant role in setting the average number of

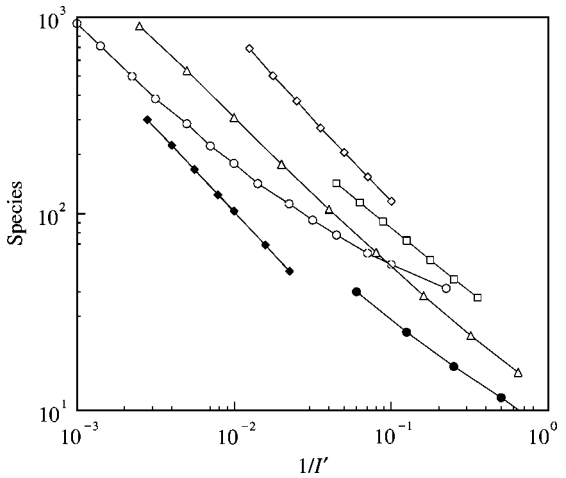

FIG. 4. Sample of plots of the stationary number of species as a function of the inverse of the immigration rate, in units of $1/\alpha$. Filled symbols refer to simulations of model (A), empty symbols are for model (B). Parameters are as follows. Filled diamonds: $N_c' = 10^{-3}$, $\beta' = 10^3$, $\gamma'_{max} = 5 \times 10^3$ (in this case the horizontal axis is $10\alpha/I$). Empty circles: $N_c' = 10^{-5}$, $\beta' = 10^2$, $c'_{max} = 20$. Empty diamonds: $N_c' = 10^{-4}$, $\alpha = 0$, $c_{max}/\beta R = 20$ (in this case the horizontal axis is $1/(\beta I)R$). Empty squares: $N_c' = 3.125 \times 10^{-7}$, $\beta' = 32$, $c'_{max} = 2$. Empty triangles: $N_c' = 10^{-5}$, $\beta' = 2$, $c'_{max} = 8$. ℓ_{maax} is either four or eight. In all cases, $N_{ini} = 4N_c$.

species at equilibrium. In the lower plateau, the dynamics is dominated by the internal ecological processes, while in the higher plateau the fast arrival of new individuals controls the species composition on the island. This latter situation is analogous to the one observed in the defaunation experiment reported in Simberloff & Wilson (1969) and Simberloff (1969). The value of S reached in the higher plateau mainly reflects the size of the finite pool. If $M \to \infty$ (provided N_h and B are large enough), it moves towards increasingly larger values of S, and the scaling behavior holds in a broader range of I.

The results for the continuous model are completely similar. The regime between the two plateaus is represented in Fig. 4. Notice that in this case we do not have a fixed continental pool, or, in other words, the parameter M has to be interpreted as infinite. Some of the curves show a curvature in log–log plots, which can be eliminated introducing S_0 as additional fit parameter and plotting $(S - S_0)$ vs. I. The effect of S_0 is thus to reduce the effective exponent a as the immigration flux is reduced.

The observed exponents range from $a = 0.42$ to 1. Interestingly, the case with $a = 1$, corresponding to a competition exponent $b = 0$ (not represented in Fig. 4), refers to a case where basal species were not in competition, since we used Model (A) with *constant* resources, $N_0(t) \equiv R$. In all other cases, the exponent b was positive.

We now discuss the behavior of biodiversity with the parameters of the ecological equations. Keeping the other dimensionless parameters given in eqns (8) and (9) fixed, biodiversity increases logarithmically with the resources R/N_c,

$$S \approx A_1 + A_2 \log(R/N_c). \tag{13}$$

This result holds for the IBM and for the continuous models, but for model (A) it is only valid in some range of parameter values. In fact, for fixed γ'_{max} and N_c' that is small enough, model (A) is found in the garden regime, where only basal species survive, and the scaling behavior is different there (see Appendix A). The exponent a, defined in eqn (10), changes only very weakly with R/N_c.

Biodiversity also increases with the maximal transfer rate, either γ'_{max} for Model (A) or c'_{max} for Model (B), when all other parameters in eqn (8) are kept constant. In the first case, at small $\gamma'_{max}N_c'$ we again reach the garden regime, where the number of species is almost independent of I. In the second case, the number of species tends to zero as c'_{max} approaches unity (for $N_{ini} = N_c$). Both limits can be interpreted as corresponding to $a = 0$, thus $b = \infty$. The exponent a then increases slowly with γ_{max}.

The effect of the parameter β', when other parameters in eqns (8) and (9) are fixed, depends on the immigration rate. While biodiversity increases for increasing β' at small immigration, the opposite happens if immigration is large. Thus, I–S curves relative to different values of β' should cross at some point. This behavior reflects the fact that the exponent a decreases with increasing β', while S_0 increases. As in the case of γ'_{max}, the decrease of a can be explained by the fact that, at larger β', the probability that a colonizer has a positive growth rate becomes smaller. The positive effect on S_0, on the other hand, is due to the fact that the larger the β', the more likely it is that

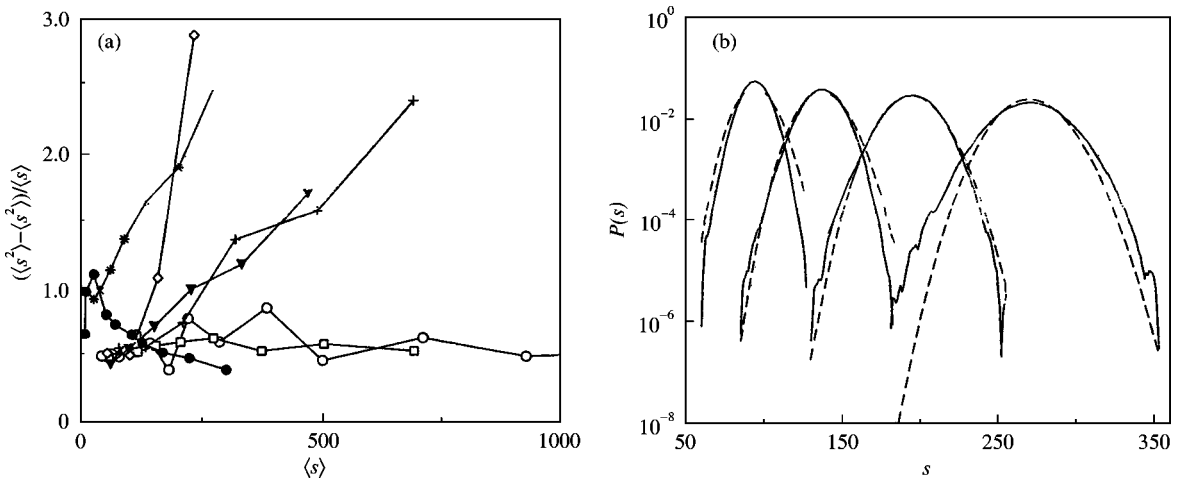

FIG. 5. (a) Ratio between the variance and the mean of the distribution of the number of species. (b) Comparison of four stationary $P(s)$ (solid lines ——) with Poissonian distributions with the same average value (dashed lines – – –). From left to right resources and immigration rates increase, other parameters are fixed. Model (B) has been used.

two predators feeding on the same prey species can coexist.

We also measured the stationary distribution $P(s)$ of the number of species s. We plot in Fig. 5 a the ratio between the variance $V_s = \langle s^2 \rangle - \langle s \rangle^2$ and the mean $S = \langle s \rangle$ as a function of the mean number of species S. The measure is much noisier than that of the average value and is strongly affected by possible sampling errors. The variance is typically lower than the mean for small $\langle s \rangle$, but at some point increases faster than the mean, becoming larger than it at large $\langle s \rangle$. Since for a Poissonian distribution the variance and the mean are equal, the distribution $P(s)$ is narrower than a Poissonian for small $\langle s \rangle$, and broader for large $\langle s \rangle$ (see Fig. 5b, where for each curve a Poissonian distribution with the same mean value has been represented as a dashed line). Notice, however, that the comparison with a Poissonian distribution is very good for some range of parameters.

4.2. SPECIES AREA RELATIONSHIP

In order to investigate te dependence between biodiversity and area, we have to fix the relationship between area and immigration rate I. Usually, a positive correlation is expected even though the actual dependence may vary with the species considered. We restrict our study to the assumption that the immigration rate is proportional to the typical cross-section of the island (MacArthur & Wilson, 1963), that is, to the square root of the total area,

$$I = I_{ct} + kA^{1/2}. \tag{14}$$

We also include a constant I_{ct} to take into account the fact that, for islands in an archipelago, the immigration rate depends much more on the geometry of the archipelago and on its distance from the mainland than on the value of the area. For isolated islands and whole archipelagos, on the other hand, there is usually a unique source of immigrants from the mainland, and the effect of area on immigration is expected to be important. In view of this situation, in the first part of the discussion the constant I_{ct} will be neglected. The parameter k is related to the distance from the mainland.

In the framework of the IBM, the other parameter influenced by area is the number of patches N_h, which is taken to be proportional to area: $N_h = A$, with an appropriate choice of units. Thus, we simulated systems with different values of N_h, varying the immigration rate as above. Our main result is that we always obtain a power-law dependence of the number of species with the area, with typical values of z in the interval 0.6–0.8, as it is observed for the case of

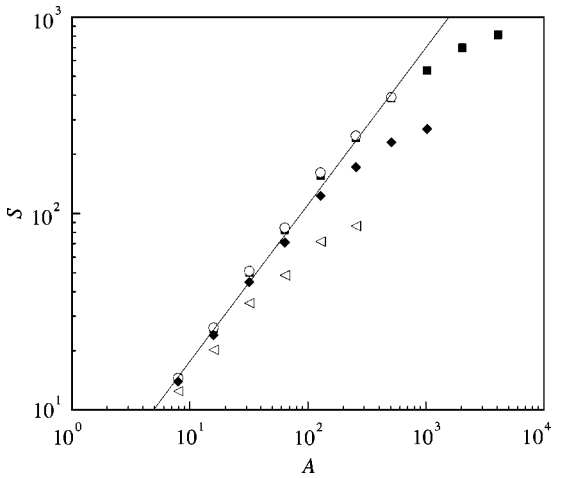

FIG. 6. Average number of species as a function of area in the IBM model, for an immigration rate proportional to the square root of A. The three curves correspond to different sizes of the species pool M, as shown in the legend. The remaining parameters are equal for the three curves and are $E = 150$, $E_{rep} = 200$, $d = 1$, $\delta = 20$, $p_d = 0.002$. The straight line has $z \sim 0.75$. These results are obtained with the cascade model. Similar curves are obtained for a random matrix, with values of S slightly below these, on the average. (■) $M = 1000$, $B = 10$; (○) $M = 1000$, $B = 5$; (◆) $M = 300$, $B = 10$; (◁) $M = 1000$, $B = 10$.

archipelagos, to which our immigration model should apply. Taking into account additional sources of immigrations, like closeby islands, is expected to reduce the dependence of the immigration rate on area, and thus to cause a decrease in the effective z values, making them more similar to the values observed in groups of neighboring islands.

For the IBM, we represent in Fig. 6 the number of species as a function of area, with immigration rate $I \equiv k\sqrt{A}$ and $N_h \equiv A$, for different values of the continental pool M. It can be seen that the species–area relationship bends for large areas, apparently tending to an asymptote. Increasing the species pool M increases the asymptote, but leaves the value of the effective exponent unchanged.

We now come to the species–area relationship in the continuous formulation of the ecological dynamics. We should first discuss how the parameters of the ecological equations, eqns (8) and (9), depend on area. The variables N_i of ecological equations have the meaning of spatial densities of individuals. Thus the equations are invariant with respect to changes of area. There is however another important determinant of the ecological dynamics: The threshold N_c below which extinctions happen. Two different cases have to be considered:

1. N_c independent of area: there is a critical density below which the species go extinct, as for Allee's effect (Allee *et al.*, 1949). Such a situation is expected, for instance, if the individual of the species is uniformly dispersed in the area A so that, below the critical density N_c, they cannot find mating partners.

In this case, the ecological dynamics is invariant under changes of the area and, in particular, the extinction rate does not depend on A. Assuming that the immigration rate increases with area as in eqn (14), and that the area is much larger than $(I_0/k)^2$, we find

$$S \propto A^z, \quad z = a/2, \tag{15}$$

where a is the exponent in eqn (10).

2. Extinctions depend on the absolute number of individuals $A \times N_i$, wherein the extinction threshold is

$$N_c \propto 1/A. \tag{16}$$

(a) First, we consider this case together with $I = I_{ct}$ independent of area [corresponding to $k = 0$ in eqn (14)]. From eqn (13), we obtain then that the number of species increases logarithmically with area:

$$S \simeq A_1 + A_2 \log(A). \tag{17}$$

This relation is indeed observed for birds in the central islands of the Solomon archipelago, which are all very close to one another (Diamond & Mayr, 1976). For such islands, the immigration rate can be expected to be rather independent of area and the logarithmic SAR is found.

(b) The immigration rate increases with island size ($A \gg (I_0/k)^2$),

$$I = kA^{1/2}. \tag{18}$$

In this case, we cannot rely on previous results, and we have to perform new simulations, scaling the parameter I as in eqn (18).

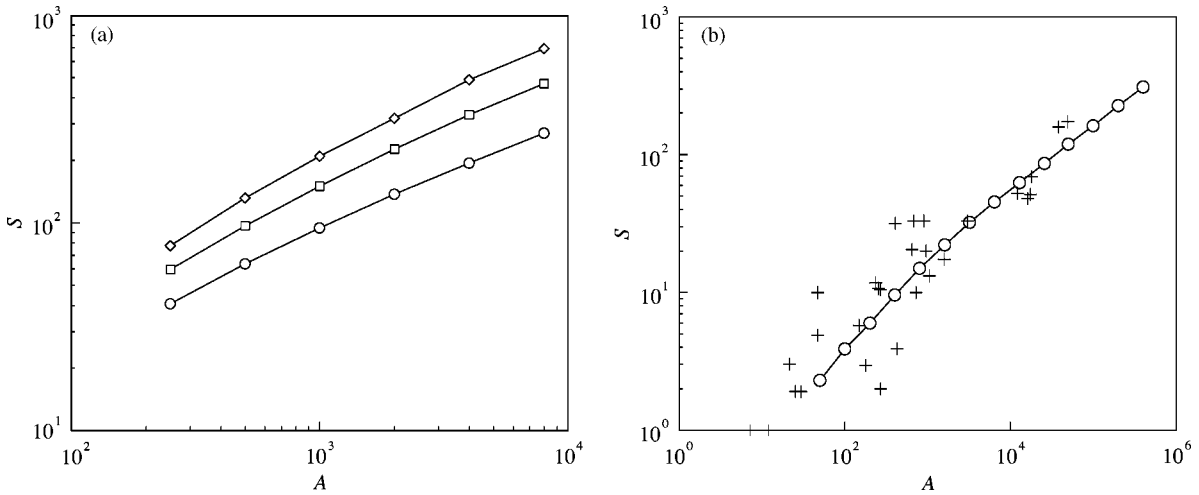

FIG. 7. Number of species as a function of area, in the hypothesis $N_c \propto 1/A$, $I = kA^{1/2}$. (a) Curves for different values of k, with $\ell_{max} = 4$. (○—○) $A^{1/2}/I' = 0.5$; (□—□) $A^{1/2}/I' = 0.1$; (◇—◇) $A^{1/2}/I' = 0.02$; (*b*) A curve for $k = 0.02$ compared to biodiversity data of Pacific archipelagos (Adler, 1992; Rosenzweig, 1995). Here, $\ell_{max} = 8$. Results are for Model (B). (○—○) Model; (+). Tropical archipelagos.

We note that, in both cases 2(a) and 2(b) model (A) can become problematic at large area. In fact, as area increases the coupling constant $\gamma_{max} N_c/\alpha$, which is inversely proportional to the area, becomes smaller, and the system will be dominated by dissipative effects if the biomass of the species is of order N_c (see Appendix A). The result is that, unless $\alpha = 0$, eqn (29) would not be satisfied as area increases, and the system would again finish in the garden regime. It is not surprising that Lotka–Volterra equations are in trouble for very low densities: in fact, they are analogous to equations of chemical kinetics, and when the density of the species that is involved becomes too small, the assumptions on which they are founded break down. To avoid such a problem, we used the ratio dependent model (B) together with eqn (18). Nonetheless, our numerical study shows that model (A) also provides comparable results in a suitable range of parameters.

Results are plotted in Fig. 7, and yield an approximately power law species area relationship for large enough values of the parameter αk. In the log–log plot, the curves $S(A)$ show a negative curvature which can be eliminated through the introduction of an extra parameter A_0 in the fit,

$$S \simeq c(k)(A - A_0(k))^{z(k)}. \tag{19}$$

Both the effective exponent $z(k)$ and the limit area $A_0(k)$ increase slowly with the immigration parameter k. For the curves in Fig. 7, the exponent $z(k)$ ranges from $z = 0.49$ at $k = 2$ to $z = 0.56$ at $k = 50$.

We notice however that the scaling form eqn (19) is only approximate, that a scaling of the form $A^z \log(A)$ would probably be more adequate, and that the immigration rate is a better scaling variable than area. But since real data are mainly obtained for the SAR, and field information about immigration rates is largely lacking, we extract a functional relation between S and R for the sake of comparison with real ecosystems.

Our model of immigrations applies to whole archipelagos or to isolated islands because we consider a single source of immigrants. It is remarkable that the exponent z observed for a set of Pacific archipelagos has the value $z = 0.54$ (Adler, 1992; Rosenzweig, 1995), in very good agreement with the results of our simulations when I scales as the square root of the area A. Real data are shown for comparison in Fig. 7b. When I is a constant independent of area, we obtain a logarithmic SAR, again in agreement with observation where, due to the geography, the hypothesis of a constant I is reasonable (Diamond & Mayr, 1976).

It is striking that models at different description levels, as the IBM and the continuous model

(B), yield very similar species–area relationships. We compared other statistical features of the individual based and the continuous models, and found that they are qualitatively very similar (this holds for the Lotka–Volterra model as long as the garden regime and the opposite low dissipation regime are avoided). In the following, we will present a complete analysis of the stationary state for data obtained from the IBM and from the continuous model (B).

4.3. DISTRIBUTION OF SPECIES ABUNDANCES

We measured distributions of species abundances, defined as the probability density $p(N)$ of species with N individuals (or total biomass equal to N in the case of the continuous model), both for the IBM and for the continuous model. We observe a good qualitative agreement of the results in both approaches.

In the framework of the IBM, we measured the distribution of species abundances for three values of the immigration rate corresponding to the three regimes in Fig. 3 (slow, intermediate and fast driving). Fig. 8 represents the frequency $p(N)$ with which species formed by N individuals were recorded. All curves show an initial fast decaying part corresponding to species that go extinct almost immediately after arriving at the island. Since these species do not find prey to feed on, their initial energy decays exponentially and they die out of starvation. The relevant part of these distributions results from species which play a role in the ecological network. This part shows a power-law decay of the form

$$p(N) \propto N^{-\xi}, \tag{20}$$

with $\xi \simeq 1$. Finally, the external resources set the value of N at which an exponential cut-off appears. Our results are in good agreement with field measures of diversity, many of which also return a power-law distribution of species abundances with an exponent in the range 1–1.25 (Pielou, 1969; Solé *et al.*, 2000).

The same results are obtained in the framework of the continuous model. In this case, however, we observe that the exponent ξ increases slowly with immigration rate, tending to $\xi \approx 1$ in the limit $I \to 0$. The maximum value that we found in our simulations is $\xi \approx 1.25$, still compatible with observational data. A sample of results is reported in Fig. 9a. In Fig. 9b the decrease of the exponent ξ with the immigration rate is shown.

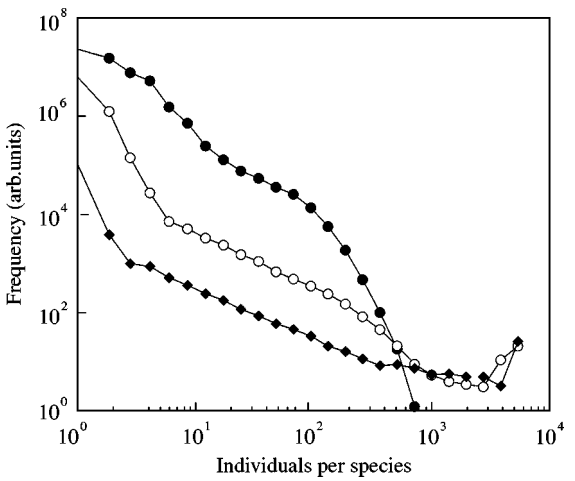

FIG. 8. Distribution of the number of individuals per species in the IBM model for different values of the immigration rate. The remaining values are as in Fig. 3. As can be seen, the abundances of species are power-law distributed with an exponent close to unity in all cases. The increase in the immigration rate moves the exponential cut-off at large sizes towards the right. (●—●) $I_0 = 1/32$; (○—○) $I_0 = 1$; (◆—◆) $I_0 = 32$.

4.4. LIFETIME DISTRIBUTION

The distribution of lifetimes of species is shown in Fig. 10 in a log–log plot, for several values of the immigration rate and of other parameters. After an initial part where the distribution is almost uniform, corresponding to species with very short permanence time, we observe an approximate power-law decay of the probability density for a range of at least one and half decade

$$p(\tau) \approx \tau^{-\eta}, \tag{21}$$

when using different parameter values, we found values of the effective exponent η between 2.1 and 2.8.

The average lifetime $\langle \tau \rangle$ in the equilibrium state is related to biodiversity through the relation

$$\langle \tau \rangle = \langle S \rangle / I \propto I^{-b/(1+b)}, \tag{22}$$

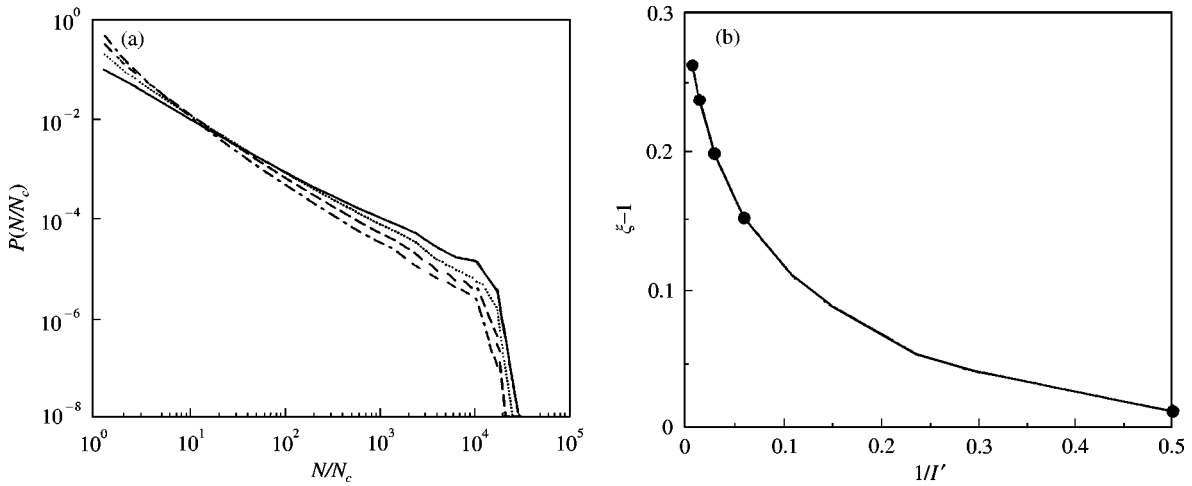

FIG. 9. (a) Distribution of the biomass per species in the continuous model (B), for different values of the immigration rate. (——) $I' = 2$; (· · · · ·) $I' = 0$; (– – –) $I' = 35$; (– · –) $I' = 125$. (b) The exponent ξ of the power-law part of the distribution minus one as a function of the immigration rate. Parameters: $N'_c = 10^{-5}$, $\beta' = 1$, $c'_{max} = 2$, $\ell_{max} = 4$.

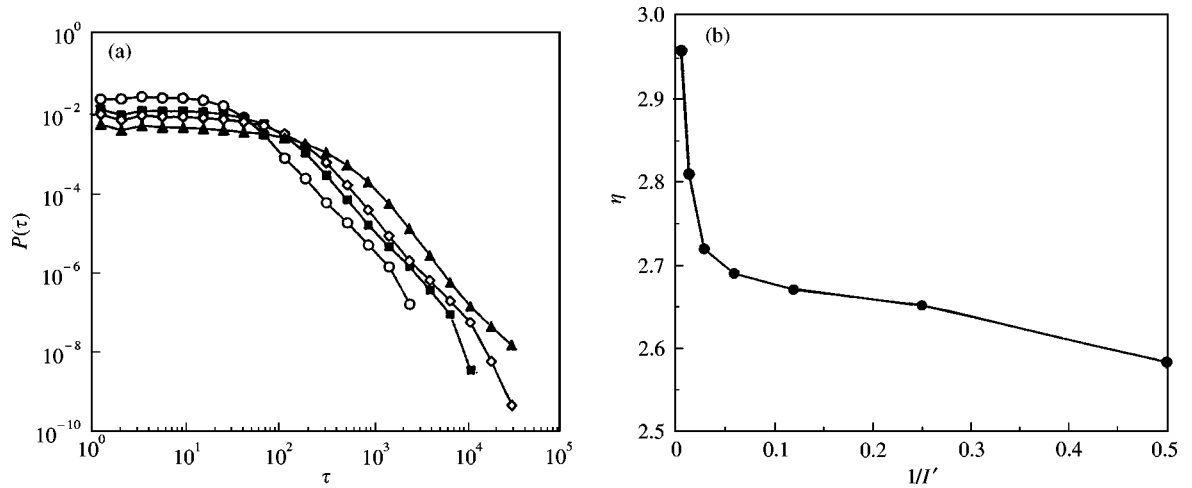

FIG. 10. (a) Lifetimes distribution in model (B) for different values of the immigration rate. Other parameters: $N'_c = 10^{-5}$, $\beta' = 1$, $c'_{max} = 2$, $\ell_{max} = 4$. (○—○) $I' = 2$; (■—■) $I' = 8$; (◇—◇) $I' = 35$; (▲—▲) $I' = 125$. (b) The exponent η for the power-law part of the distribution as a function of the immigration rate. Other parameters as in (a).

which follows from its definition and from the condition of stationarity. The average lifetime decreases with the immigration rate I and, consistently, the value of the exponent increases, as it is shown in Fig. 10b.

Our results compare qualitatively well with measured patterns (Keitt & Marquet, 1996; Keitt & Stanley, 1998). It was in fact observed that the time of permanence of birds in local patches follow a distribution approximately of the form (21) with effective exponent $\eta = 1.6$, indeed smaller than the typical values found in our simulations. A result which compares better to this last value has been found, using a model without explicit ecological dynamics, in Solé *et al.* (2000).

4.5. NETWORK ORGANIZATION

The structure of the ecological network changes, even if very slowly, with changing immigration rate. We have examined in particular the

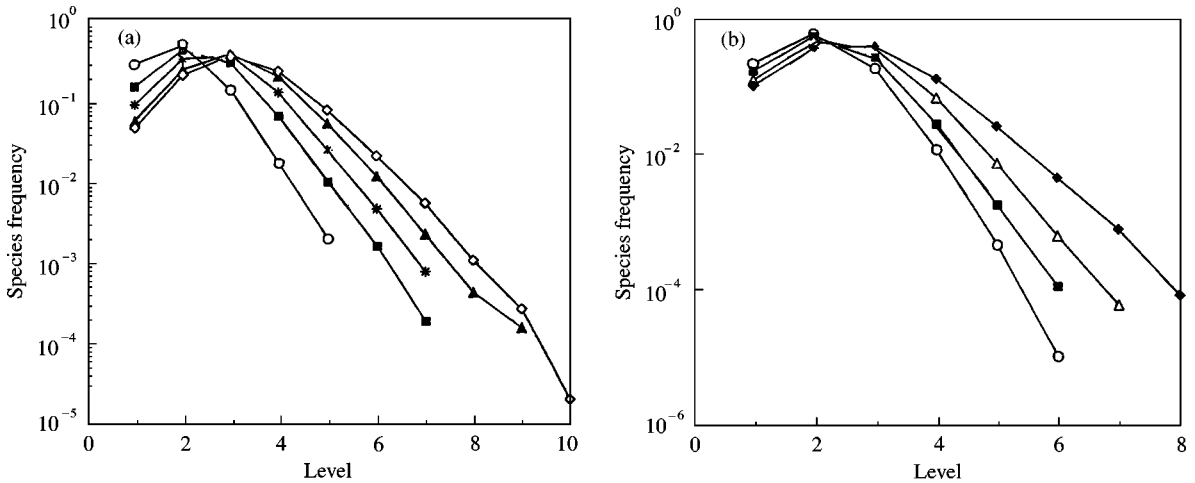

FIG. 11. (a) Frequency of species at trophic level l in the entire course of the simulation for model (B) and different values of the immigration rates. Food chains become longer at increasing immigration rate. (○—○) $I' = 2$; (■—■) $I' = 7$; (∗—∗) $I' = 15$; (▲—▲) $I' = 30$; (◇—◇) $I' = 45$. (b) Similar, for different values of the resources. (○—○) $R/N_c = 10^6$; (■—■) $R/N_c = 10^5$; (▲—▲) $R/N_c = 10^4$; (◆—◆) $R/N_c = 10$;

number of trophic levels, the number of links per species and the total biomass.

We define the trophic level of a species as the minimal path (number of links) connecting it to resources. In all our simulations the number of trophic levels varies between four and ten. It shows a tendency to increase with immigration rate, as it is illustrated in Fig. 11.

The average number of links per species, counted as average number of preys, is shown in Fig. 12 as a function of the immigration rate. It changes very slowly (logarithmically) and, in some cases, in a non-monotonic way (for most curves we only observe either the increasing or the decreasing part). A similar pattern is observed as a function of the resources R (see Fig. 12b). Thus, as a function of the number of species, the number of links per species behaves non-monotonically. It also depends weakly on the maximum number of links allowed when the new species is added to the ecosystem, ℓ_{max}. The total biomass also increases approximately as a power law of the immigration rate, as shown in Fig. 13. The exponent ranges from 0.15 to 0.58.

5. Relationship to MacArthur & Wilson's Theory

We have already seen in the previous section that quantitative biodiversity patterns can be derived from a balance between external driving (immigrations) and the intrinsic population dynamics of the ecosystem. Here, we would like to relate these results to the existing phenomenological approaches, in particular MacArthur & Wilson's (1963, 1967) theory of island biogeography.

In an ensemble average (or, equivalently, in an average over long times), the response of the system to a constant immigration flux I translates into a stationary extinction rate E. This can be expressed as a function of the average number of species S in the system, $E = E(S)$. Of course, this function depends also on the model parameters and on qualitative features of the immigration flux. Since the system is at a stationary state, immigration and extinction balance on the average,

$$I - E(S) = 0, \tag{23}$$

as postulated by MacArthur & Wilson. The net immigration flux here measures the average number of *new accepted species* per unit of time. The functional form of the *extinction curve* $E(S)$ can now be obtained from the underlying population dynamics. As explained above, we find

$$E(S) = E_0 S^{1+b}, \tag{24}$$

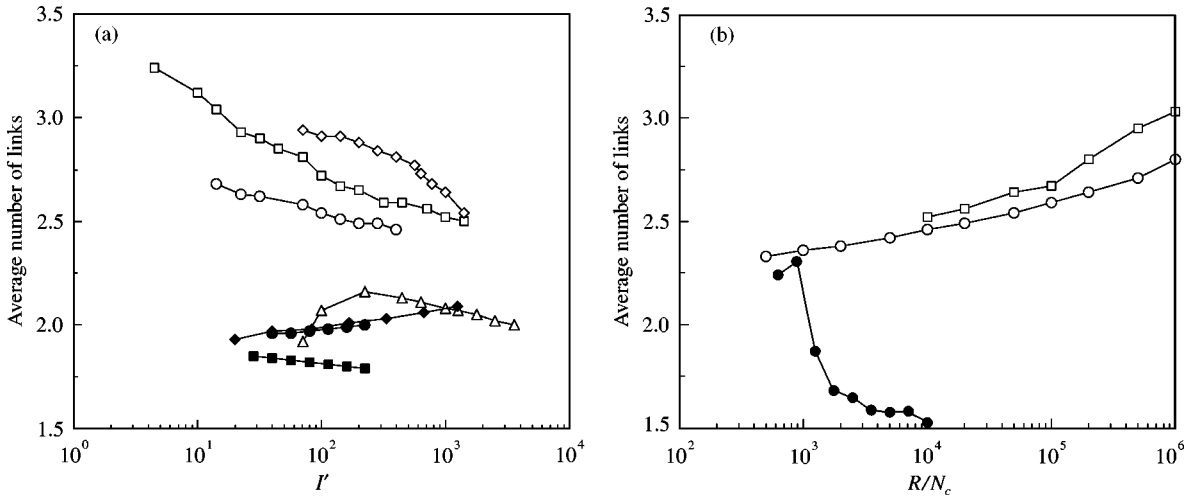

FIG. 12. (a) Number of links per species as a function of the immigration rate for model (B). Empty symbols refer to $\ell_{max} = 8$, filled symbols to $\ell_{max} = 4$. (b) Same as a function of the resources R.

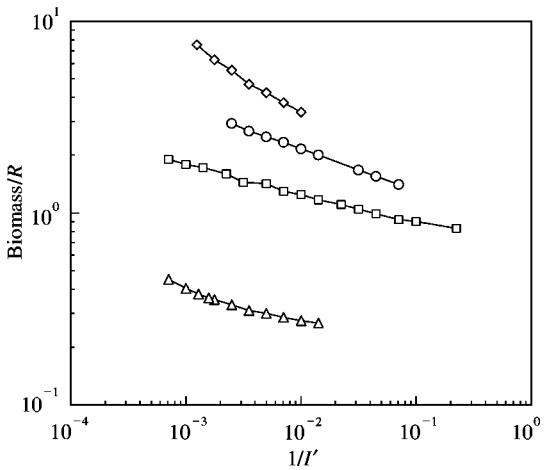

FIG. 13. Biomass as a function of the inverse of the immigration rate in the continuous model (B).

in the scaling regime where the number of species increases as a power law of the immigration rate. The competition exponent b has been introduced in eqns (11) and (12). In fact, from the stationary solution of eqn (23), we recover eqn. (10),

$$S = \left(\frac{I}{E_0}\right)^{1/1+b}. \tag{25}$$

This equation allows to derive the exponent z of the species–area relationship. We can now assume an arbitrary scaling of the immigration rate and the factor E_0 with the area,

$$I \propto A^s, \quad E_0 \propto A^{-\varepsilon}, \tag{26}$$

in order to obtain a general SAR and a relation among all the scaling exponents involved,

$$S \propto A^z \quad \text{with} \quad z = \frac{s+\varepsilon}{1+b}. \tag{27}$$

For the population models, we assumed $s = 1/2$ (the immigration rate is considered proportional to the linear size of the island), and we obtained $\varepsilon = 0$ (in fact, the number of species increases as does the logarithm of R/N_c at fixed I, both in the IBM and in the continuous model (B)). The case of immigration flux independent of area constitutes a marginal situation in which $s = 0$, implying $z = 0$ and a logarithmic dependence (at most) of A with S.

We remark here that, as in the explicit population models, we are assuming that the only source of immigrants is a continent far apart. The exponents that we find should then be compared to the exponents observed for isolated islands or archipelagos, while the exponent computed among islands of the same archipelago is expected to be lower, due to a reduced dependence of immigration rate on area. Another point to

remark is that the net immigration rate I measures the flux of new species arriving at the island. If this flux is assumed to originate from a continent of M species, I can be related to the bare immigration flux I_0 by correcting for the immigrant species already present on the island. The simplest ansatz is $I(S) = I_0(1 - S/M)$ (MacArthur & Wilson, 1963, 1967). Expressed in terms of I, the average number of species S reaches a saturation value of order M. If the pool of immigrants is very large, $M \gg S$ or infinite, as assumed in the continuous model, this correction is negligible.

6. Summary and Conclusions

We have presented a study of biodiversity in insular ecosystems at the individual and the population level. Our interest has been focused on the statistical properties of the dynamical stationary state and on the scaling relations between the system variables. Instead of describing detailed situations in which some particular species and their exact interactions with their known preys and predators are included, we let ecological networks self-organize through random assemblage of species, ecological dynamics, and possible extinctions.

Our main result is that, in a broad range of parameters, biodiversity scales approximately as a power law of the immigration rate. The value of the exponent varies slightly when the parameters of the models are changed, but the qualitative features of the stationary state are quite robust.

The behavior of biodiversity with immigration rate allows to derive a species–area relationship with a power-law shape, if we assume that an allometric relation between the area of the island and immigration rate exists. If the immigration flux is independent of the area, we recover a logarithmic SAR (Diamond & Mayr, 1976). Such a model of immigration considers as unique source of diversity a flux of species from a continent far apart. We have numerically analysed the case where the immigration flux scales as the square root of the total area of the island, and compared our results to observations in isolated islands or whole archipelagos. The agreement is in this case rather good: the observed value of the effective exponent z on archipelagos is $z = 0.54$ (Adler, 1992; Rosenzweig, 1995), while we typically get, with the continuous model, values between 0.52 and 0.56 and, with the individual based model, values between 0.6 and 0.8. Thus, the comparison of our two description levels points out to species–area law of the type (1) as a generic feature of a broad set of ecological models with random interactions.

Our models qualitatively reproduce other features observed in real ecosystems. We observe a power law distribution of population abundances, i.e. the number $p(N)$ of species with N individuals approximately decreases as $p(N) \propto N^{-\xi}$. This is expected to be a general consequence of the multiplicative nature of population dynamics equations. The exponent ξ found in our simulations is close to unity, in favorable comparison with field data, and increases with the immigration rate.

We also observe a broad distribution of the time of permanence of species in the system τ, as it has been observed in the field (Keitt & Marquet, 1996; Keitt & Stanley, 1998) and in a related model (Solé *et al*., 2000). The average permanence time is proportional to the number of species and inversely proportional to the immigration rate, $\langle \tau \rangle = \langle S \rangle / I$, so that it decreases with the immigration rate. The fact that it is observed, both in field studies and in models, that its distribution is broad, could help to reconcile the apparent dichotomy between fugitive and permanent species (Schoener & Spiller, 1987): These two groups could correspond to the two extreme cases of a unique distribution of permanence times. The approximate power-law shape of the distribution of times of permanence on the island is reminiscent of the analogous distribution of the lifetime of genera in the fossil record, which is approximately given by $P(\tau) \propto \tau^{-\eta}$, with $\eta \approx 2$, close to what is observed in our model for very small immigration rates and also close to ecological observations. It is tempting to speculate that this similarity points out at similar mechanisms acting on the time scales of ecosystem dynamics as on the time scales of macroevolution.

The number of trophic levels in the food web is also strongly influenced by the immigration rate.

We typically find from four to ten trophic levels, depending on parameters, and with a tendency for the number of levels to increase with immigration rate. Hints to the correlation between immigration rate and the number of levels can be found in the fact that the length of food chains appears to be positively correlated to habitat area, although the data are quite poor (Schoener, 1989; Spencer, 1997). Our results suggest that one of the factors limiting the length of food chains is the immigration or speciation rate. Notice that in our model no other limitations to the length of food chains exist: energetic considerations would limit the number of levels to a value $\log(R/N_c)$, much larger than the one observed.

An important result of our study is that the observed statistical patterns are rather robust with respect to changes in the dynamical rules of the model. One example is the representation of space. Although one could think that explicit space is in any case needed in order to recover a satisfactory SAR, we included space only in an effective way, suggesting that its effect is mainly translated in an increase of the immigration rate and the resources with the area. We believe that this effective approach captures the main features of the behavior of biodiversity with area, even if important issues, like for instance the presence of many different habitats, are not represented in the model.

As Pimm poses it, (…) *it is pointless to try to justify models' equations biologically – their assumptions are almost bound to be wrong.* (…) *The concern should not be whether the assumptions are wrong* (*they are*!), *but whether it matters that they are wrong.* (Pimm, 1991). It seems that the statistical laws and the scaling relationships that we observed are generic properties of complex ecosystems, that is the unavoidable results of a minimal set of rules governing population dynamics and immigrations. Thus, the strategy is to look for the simplest set of rules which appear sensible and which allow to derive the observed statistical patterns of biodiversity.

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APPENDIX A

The Garden Regime

In the case of model (A) of continuous dynamics, we observed that only basal species can survive on the long run for a certain range of parameter values. In this case, the stationary state is reached over time scales much longer

than the typical time scales of our simulations (see Fig. 14).

We call such a state the *garden regime*, since predators are absent. Its statistical properties are peculiar: the distribution of biomasses is narrow and peaked at very low values ($N_i \simeq N_c$, $\forall i$), and the distribution of lifetimes is bimodal, with a high peak for very short lifetimes corresponding to transient species, and a lower one for large lifetimes, corresponding to semi-permanent species. Finally, the distribution of the transfer rate γ_{0i} from the external resources to species i is strongly peaked close to the maximum allowed value γ_{max}. All these features can be easily rationalized as follows.

Let us consider a situation where S basal species coexist feeding on the abiotic resources N_0. Our calculations (unpublished) show that at the static fixed point of the corresponding ecological equations, [eqns (3) and (4)], all biomasses are positive if and only if all differences in the coefficients γ_{0i} are smaller than Γ/S, where $\Gamma = \gamma_0 \beta R/\alpha$. Thus, as S increases, the coupling constants between the basal species and the environment deviate from the initial distribution and become more and more similar. Notice that, if $\beta = 0$, the coefficients γ_{0i}'s should be exactly equal to guarantee coexistence (this expresses in this context the "principle of competitive exclusion"). This conclusion does not vary qualitatively if one considers Model (B) instead of Model (A). Thus, in a system without predators and high immigration of basal species, we expect to find many basal species with very similar biomasses, all of the order R/S (S is necessarily smaller than R/N_c) and coefficients γ_{0i} very near in value.

Let us now consider the arrival of a predator to such a system, considering first Lotka–Volterra equations (model (A)). The growth rate of the predator is bounded from above

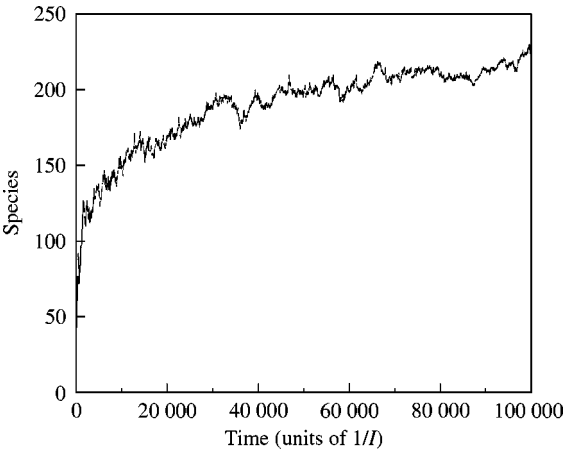

FIG. 14. Evolution of the number of species in the garden regime. Notice that, although the rate of increase gets slower, the number of species does appear to reach any stationary value. Model (A) has been used. Parameters: $\gamma N_c/\alpha = 0.1$, $\beta' = 10$, $N_c' = 0.001$, $\ell_{max} = 4$.

by r_{max},

$$r_{max} = \ell_{max}\gamma_{max}\frac{R}{S} - \alpha - \beta N_c. \qquad \text{(A1)}$$

Since R/S is larger than N_c, we find that, for large S, a non-basal species can colonize only if

$$\gamma_{max} \geqslant \frac{1}{\ell_{max}}\left(\frac{\alpha}{N_c} + \beta\right). \qquad \text{(A2)}$$

Every time we observed in our simulations ecosystems mainly composed of basal species and whose biodiversity has a time behavior similar to that in Fig. 14, the above condition was not fulfilled.

In model (B), $r_{max} = \ell_{max}\alpha' c_{max} - \alpha - \beta N_c$. This quantity must be larger than zero, otherwise no species would survive. Thus, the garden regime that we described in this appendix can always be invaded by predators in simulations of ratio dependent PFR (unless we use different parameters for basal and predatory species).