

Evolving biodiversity

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Abstract

We formulated a mathematical model to study the evolution of biodiversity. Our model describes a collection of sites and incorporates a simple but explicit description of the competitive processes within a site. In our model the characteristics of component species evolve towards an evolutionarily stable state and in this way an evolutionarily stable assemblage of species is formed. We show that the number of species in these assemblages matches two well-documented patterns in biodiversity: the increase in the number of species towards the equator and the dependence of the number of species on the productivity of habitat: the average number of species rises to a maximum and then falls when plotted against increasing productivity of that habitat. Our results show that population dynamical and evolutionary processes can underlie patterns in biodiversity.

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INTRODUCTION

The distribution of species over the earth is not even or random but seems to follow certain distinct patterns. Probably the best known example of such a pattern is the increase in the number of species towards the equator (Rosenzweig 1995; Gaston & Williams 1998). Another pattern is the dependence of the number of species on the productivity of habitat; the average number of species rises to a maximum and then falls when plotted against increasing productivity of that habitat (Rosenzweig 1995). Such patterns in biodiversity are well documented but as yet not unequivocally explained.

Most species do not exist in isolation but coexist and compete with other species. Although communities of competitive species can harbour a large number of species (Zobel 1992), theoretical results predict that the number of competing species is limited by the number of resources. This apparent paradox has been explained by models that describe a collection of sites or patches in which the different species interact. Competing species that cannot coexist in a single site can coexist in a collection of coupled sites, and in this way many species can coexist in the collection of sites, despite the fact that local competition is for a small number of resources (Hastings 1980; Tilman *et al.* 1994; Tilman 1994; Nowak & May 1994; May & Nowak 1994; Lehman and Tilman 1998).

The number of species that can coexist somehow depends on the species' characteristics. In most models for biodiversity these characteristics are predefined constants. In real communities, however, the characteristics to a certain extent are formed through evolution. It is still very

much an open question how the properties of competitive communities emerge through the evolution of their component species (Levin *et al.* 1997). Here, we employed the concept of evolutionary stability (Maynard Smith 1982) to gain insight into the evolution of biodiversity through the evolution of assemblages of species.

Most models of competitive communities (Hastings 1980; Tilman *et al.* 1994; Tilman 1994; Nowak & May 1994; May & Nowak 1994; Lehman and Tilman 1998) are based on the assumption that, within a patch, a superior competitor immediately replaces an inferior competitor. Therefore a mutant that is a marginally better competitor will immediately replace its ancestral wild type assuming they occupy the same patch, and eventually will replace the wild type's entire population (Nowak & May 1994), and all types gradually evolve towards maximal competitiveness. No assemblage is evolutionarily stable, and biodiversity will not be maintained under evolution unless types that are much less competitive appear continuously through mutations (Nowak & May 1994; May & Nowak 1994; Lehman and Tilman 1998). The creation of very different types through mutation is plausible for pathogens, but seems unlikely for organisms in which the competitive abilities are controlled by many genes.

To maintain biodiversity we relaxed the assumption of immediate replacement. To do so we employed a model that is detailed enough to describe both the interaction between types or species which are rather different and between wild types and closely related mutants. In order to describe the within patch dynamics in detail we used a "haystack" model (Maynard Smith 1964). Our model relates to and extends previous models with a description

of within patch dynamics (Cohen & Eshel 1976; Comins *et al.* 1980, Geritz *et al.* 1999) for a competitive community of self-pollinating plants that inhabit a large collection of patches. It is assumed that throughout the season the plants compete within a patch for a single resource. At the end of the season, plant biomass is converted into seeds. We assumed a trade-off between within patch competitive ability and fecundity, such that good local competitors are bad colonisers (Tilman 1997). All seeds are distributed randomly over the patches. Evolution enters via a small probability that a seed is a mutant, in which case its growth rate and fecundity is slightly different from its parent. We solved the model to find the number of types that can coexist in an evolutionarily stable assemblage.

METHODS

Model description

To analyse evolutionary stability a measure of fitness is needed, which we will derive from the population dynamics. To do so, we follow Metz *et al.* (1992, 1996) and consider two types: an abundant resident and a rare mutant that only differ in a particular trait. The interaction within a season between these two types takes place in a large number of patches, which are seeded at the beginning of the season. Whenever a patch is seeded by both types we assume that the types compete within a patch for a single resource according to the Lotka-Volterra competition model for a single resource (Hofbauer & Sigmund 1998). The model uses the variables and parameters given in Table 1.

The amount of biomass of the resident (V) and the mutant (V^*) changes throughout the season as:

$$\begin{aligned} \frac{dV}{dt} &= \left[m - \left(\frac{V + V^*}{c} \right) \right] V \\ \frac{dV^*}{dt} &= \left[m^* - \left(\frac{V + V^*}{c} \right) \right] V^* \end{aligned} \quad (1)$$

where the parameter c describes the quality of the patches and m, m^* ($m, m^* > m_{\min}$) represent the initial growth rates of, respectively, the resident and the mutant. As it turns out, the type with the largest initial growth rate is also the best competitor within a patch. Throughout this paper we will therefore refer to a type with a large initial growth rate as a competitive type. (Note that because of the redistribution of seeds a type that is locally the best competitor within a season need not be the best competitor over the seasons.)

If a patch contains only resident seeds the dynamics are given by a logistic equation with equilibrium $\tilde{V} = cm$. This reflects the fact that a type which grows faster is likely to

Table 1 Variables and parameters used in the model.

Variables	
V	Resident's standing biomass in a patch
V^*	Mutant's standing biomass in a patch
$S(t)$	Total standing biomass in patch at time t
$F(t)$	Fraction of mutant standing biomass at time t
\tilde{V}, \tilde{V}^*	Equilibrium density of resident and mutant biomass
N	Average nr. of resident seeds per patch
\tilde{N}	Average nr. of residents seeds per patch in equilibrium
N^*	Average nr. of mutant seeds per patch
t	Time within a season
m	Initial growth rate of resident biomass
m^*	Initial growth rate of mutant biomass
m_{\min}, m_{\max}	Minimum, maximum values of initial growth rate
\tilde{m}	Evolutionarily stable growth rate
c	Quality of the local environment
k, k^*	Amount of biomass of resident and mutant at beginning of season
$T(m)$	Fecundity as function of the growth rate
$W(m^*, m)$	Fitness as a function of mutant and resident growth rates
ω	Conversion factor from biomass to seeds
τ	Length of season

have more standing biomass. We made the additional assumption that the growth of biomass is fast compared with the length of the season, so that at the end of a season of length τ the amount of biomass can be approximated by the equilibrium density, hence $V(\tau) \approx \tilde{V}$. Similarly, if a patch is only seeded by mutant seeds the mutant's biomass at the end of the season will be approximately given by the mutant's equilibrium density $\tilde{V}^* = cm^*$.

If a patch contains both resident and mutant seeds the type that is locally most competitive, i.e. the type with the largest growth rate, will replace the other type if the season would last indefinitely. However, in seasons of finite length the exclusion will not be complete. To approximate the amount of biomass at the end of the season we introduce as new variables the total amount of biomass $S = V + V^*$ and the fraction of mutant biomass $F = V^*/S$. These new variables change over time as

$$\begin{aligned} \frac{dS}{dt} &= \left[m(1-F) + m^*F - \frac{S}{c} \right] S \\ \frac{dF}{dt} &= (m^* - m)F(1-F) \end{aligned} \quad (2)$$

The latter equation can be solved to give

$$F(t) = \frac{k^*}{ke^{(m-m^*)t} + k^*}$$

where k and k^* are the respective biomass of resident and mutant at the beginning of the season (which we assumed to be proportional to the number of seeds). Because the growth of biomass is fast compared with the length of the season we can use a quasi steady state approximation for the total amount of biomass, hence: $S(t) \approx c[m + (m^* - m)F(t)]$. We can thus approximate the biomass of the mutant at the end of the season as $V^*(\tau) = F(\tau)S(\tau) \approx F(\tau)[\tilde{V} + (\tilde{V}^* - \tilde{V})F(\tau)]$. This approximation works well for seasons of sufficient length (Fig. 1).

At the end of the season all biomass is converted into seeds. We assume a trade-off between fecundity and local competitiveness, such that in the absence of local competition a less competitive type produces more seeds than a highly competitive type. The fecundity per amount of biomass is given by

$$T(m) = \omega \frac{m_{\max} - m}{m}$$

where m_{\max} is the growth rate at which no seeds are produced and ω is the conversion factor from biomass

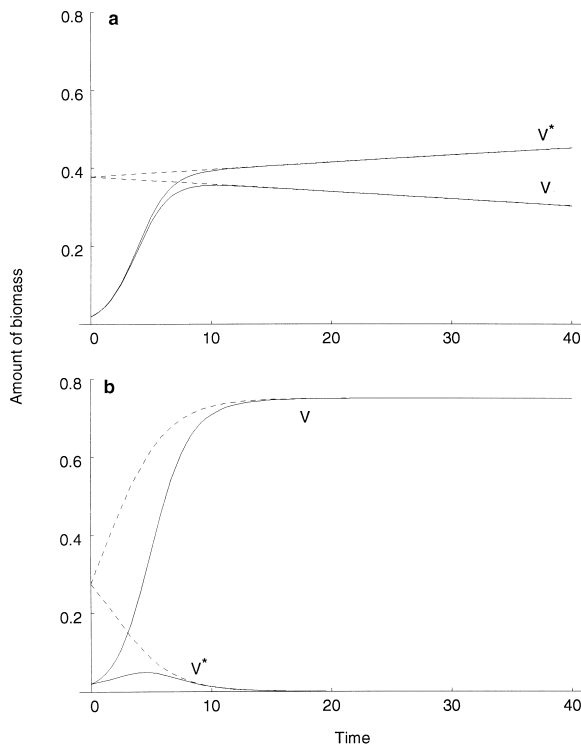


Figure 1 Exact, eqn. (1), and approximated solutions for the biomass growth in a patch. The graph shows solutions for $k=k^*=1$ and $c=50$. In (a) $m^*=0.76$, $m=0.75$, in (b) $m^*=0.35$, $m=0.75$. The drawn lines are the exact solutions, the dashed lines the approximations. The approximation works well for seasons of sufficient length. Note that the exclusion by a similar mutant takes very long but that a very different mutant is excluded rapidly.

to seeds. A possible justification for this trade-off is that plants can set aside a part of their assimilates in storage tissue, for instance a pen root, which they can remobilise when they set seed. If the amount of stored biomass is proportional to the amount of standing biomass, the amount of seeds of a type at the end of the season is $T(m)V(\tau)$ for the resident and $T(m^*)V^*(\tau)$ for the mutant.

Next we describe the dynamics over the seasons. Let N denote the average number of resident seeds in a patch. If seeds are distributed randomly and if the number of patches is large, the number of seeds per patch will follow a Poisson distribution. We first consider the case in which there are no mutants. The fraction of patches with at least one resident seed is given by $1 - e^{-N}$. In every patch the resident produces $T(m)\tilde{V} = c\omega(m_{\max} - m)$ seeds. In the next season the average number of seeds per patch is therefore given by

$$N = T(m)\tilde{V}(1 - e^{-N}) \quad (3)$$

The dynamics of N go to a unique and stable equilibrium if $T(m)\tilde{V} > 1$, which we denote by \tilde{N} .

Evolutionary analysis

The seasonal dynamics of the two types can be formulated similarly. However, here we are mainly interested in the dynamics of a rare mutant because the fitness of the mutant in a population dominated by the resident is the population growth rate of the mutant when it is rare and when the resident is at its equilibrium value \tilde{N} (Metz *et al.* 1992). We will therefore formulate the dynamic of a rare mutant directly. Let N^* denote the average number of mutant seeds per patch. If the mutant is rare the fraction of patches with more than one mutant seed is negligible and the probability of receiving one mutant seed is approximately N^* . The linearised dynamics of a rare mutant therefore read $N^{*t} = N^*W(m^*, m)$ where

$$\begin{aligned} W(m^*, m) &= \sum_{k=0}^{\infty} T(m^*)V^*(\tau) \frac{e^{-\tilde{N}}\tilde{N}^k}{k!} \\ &\approx \sum_{k=0}^{\infty} T(m^*)F(\tau)[\tilde{V} + (\tilde{V}^* - \tilde{V})F(\tau)] \frac{e^{-\tilde{N}}\tilde{N}^k}{k!} \end{aligned}$$

is the fitness of a mutant with trait m^* in a resident population with trait m [note that because the mutant is rare we only consider patches with one mutant seed, hence $k^*=1$ and $F(\tau)$ only depends on the number of resident seeds, k].

The fitness depends on the trait value of the mutant and of the wild type. The fitness function can be conveniently visualised in a pairwise invasibility plot (Metz *et al.* 1992),

which depicts the parameter combinations for which a mutant can invade a resident population (Fig. 2). The evolutionary singularities and the convergence and evolutionary stability of the singularities can be easily determined from such a plot (Metz *et al.* 1996, Geritz *et al.* 1998). Figure 2 shows that a process of adaptation through evolution by small mutation steps leads either to the minimum growth rate or to a relatively large evolutionarily stable growth rate. In some cases, the latter can become evolutionarily unstable and adaptive radiation occurs in which two disjunct types are formed from a single type (Metz *et al.* 1992, 1996; Geritz *et al.* 1997; Kisdi 1999). The evolutionarily stable growth rate \tilde{m} can also be determined analytically through evaluation of the conditions for evolutionary stability:

$$\left. \frac{\partial W(m^*, \tilde{m})}{\partial m^*} \right|_{m^* = \tilde{m}} = 0$$

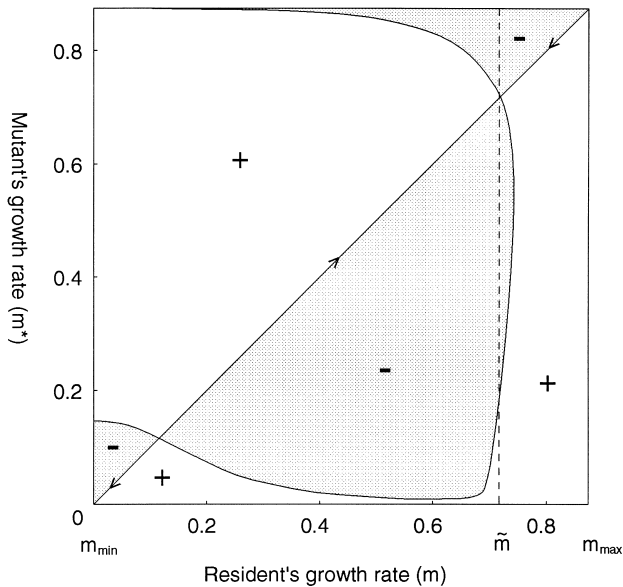


Figure 2 A pairwise invasibility plot for the interaction between wild type and mutant. The regions where a mutant's fitness exceeds unity (denoted +) and regions where fitness is smaller than unity (grey, denoted -) are plotted against the wild types and mutant's growth rate for $\tau = 10$ and $c = 8$. The lines in this plot are the curves where $W(m^*, m) = 1$. If mutation causes a small change in the trait value, mutants will have trait values close to the diagonal. Consecutive replacements will gradually change the value of the growth rate. The direction of the evolutionary change depends on the sign structure around the diagonal, evolution can lead to m_{\min} or the evolutionary attractor \tilde{m} . If the wild type's growth rate equals \tilde{m} this state is locally evolutionarily stable because no mutants with a similar growth rate can invade and convergence is stable, because in the neighbourhood of the attractor, evolution with small mutation steps will lead towards the attractor.

and

$$\left. \frac{\partial^2 W(m^*, \tilde{m})}{\partial m^{*2}} \right|_{m^* = \tilde{m}} < 0$$

(Maynard Smith 1982). The first condition can, by evaluating the partial derivative and by using the equilibrium condition for the resident, after some tedious but straightforward algebra, be rewritten as

$$\tilde{m} = (\tilde{m}\tau - 1)(m_{\max} - \tilde{m}) \left[1 - \frac{\text{Ei}(\tilde{N}) - \gamma - \ln \tilde{N}}{e^{\tilde{N}} - 1} \right] \tag{4}$$

where $\gamma = 0.5772 \dots$ is Euler's constant, and

$$\text{Ei}(x) - \gamma - \ln x = \int_0^x \frac{e^t - 1}{t} dt = \sum_{i=1}^{\infty} \frac{x^i}{ii!} \tag{5}$$

(Abramowitz & Stegun 1965).

The evolutionarily stable growth rate \tilde{m} depends on c through \tilde{N} . Equation (4) has either zero, one or two real roots for every c . If it has two real roots numerical evaluation of the second condition shows that the root with the smallest numerical value is always evolutionarily unstable, whereas the root with the largest value is evolutionarily stable except for a very small range of parameters for which we found adaptive radiation. There exists at most one evolutionarily stable growth rate $\tilde{m} > m_{\min}$ in an interaction between two types.

The evolutionary stability only holds locally and the coexistence of two types, one of which with growth rate \tilde{m} is possible, if the growth rate of the second type is much smaller than \tilde{m} [coexistence is possible if a type with growth rate \hat{m} can invade in a population with growth rate \tilde{m} and a type with growth rate \tilde{m} can invade in a population with growth rate \hat{m} . This can be deduced from Fig. 2 by considering whether invasion is possible for (\hat{m}, \tilde{m}) and (\tilde{m}, \hat{m}) pairs. Coexistence is possible for all (\hat{m}, \tilde{m}) that lie on the part of the dashed line that is situated in the + region]. Because the fraction of the type with growth rate \tilde{m} , F , changes logarithmically and $\hat{m} \ll \tilde{m}$, the exclusion of this type is fast and the immediate exclusion scenario is recovered: the population dynamics of the superior competitor is virtually unaffected by the presence of weaker competitors, while the latter perceive the presence of the superior competitor as a reduction in the number of patches that are effectively available. This can also be expressed as a scaling of the quality of the local environment, c , with the fraction of patches that do not contain seeds of the superior competitor $e^{-\tilde{N}}$. The reduction on the number of patches that is caused by the presence of a stronger competitor acts in the same way as a reduction of the quality of the environment.

The growth rate of the second type, \tilde{m} , can adapt in a

similar way in a process of repeated invasion and takeover by a third, mutant type. (Note that no mutant which is similar to the superior competitor with growth rate \tilde{m} can possibly replace it.) The evolutionarily stable growth rate of the second type, with growth rate \tilde{m} , can be determined easily by realising that it is the same as that of the superior competitor in a smaller number of effectively available patches, which is equivalent to a poorer environment. The evolutionarily stable growth rate of the second type is the same as that of the superior competitor in an environment in which the quality of the environment equals $ce^{-\tilde{N}}$. This argument can be applied iteratively to find the evolutionarily stable growth rates \tilde{m}_i of all types in the evolutionarily stable assemblage by scaling the parameter c to $c_i = c \exp(-\sum_{j=1}^{i-1} \tilde{N}_j)$, where \tilde{N}_i is the equilibrium density of the type with growth rate \tilde{m}_i . The maximum number of types in the evolutionarily stable assemblage is determined by applying this procedure until no further evolutionarily stable growth rate $\tilde{m}_i > m_{\min}$ exists.

RESULTS

Simulation runs of a version of this model that can accommodate a large number of types, show that different types can coexist, as they can in other biodiversity models (Hastings 1980; Tilman *et al.* 1994; Tilman 1994; Nowak & May 1994; May & Nowak 1994, Lehman and Tilman 1998), and diversity is possible despite the fact that the local competition is for a single resource (Fig. 3). Due to mutation and selection the growth rates adapt and hence the diversity evolves. In our model biodiversity is maintained under evolution based on small mutation steps and it can be both ecologically and evolutionarily stable. The evolutionary dynamics can cull types until a stable assemblage is reached (Fig. 3a), or biodiversity can increase by the creation of a polymorphism through adaptive radiation (Fig. 3b). Although many assemblages are possible that are ecologically stable, most of these are not evolutionarily stable. Our approach differs from that taken in most other biodiversity models in that we concentrate on the evolutionarily stable assemblage.

We determined the value of the evolutionarily stable growth rates by the method described in the previous section. The composition of the stable assemblage depends on the quality of the environment and the length of the season. In very poor environments and short seasons evolution is towards a common type with minimal competitive abilities (Fig. 4a). In slightly richer environments a single, more competitive type evolves. The evolutionarily stable growth rate of this type increases with the quality of the local environment. The reason for this is that in richer environments the equilibrium density is higher, hence fewer patches remain empty so that local

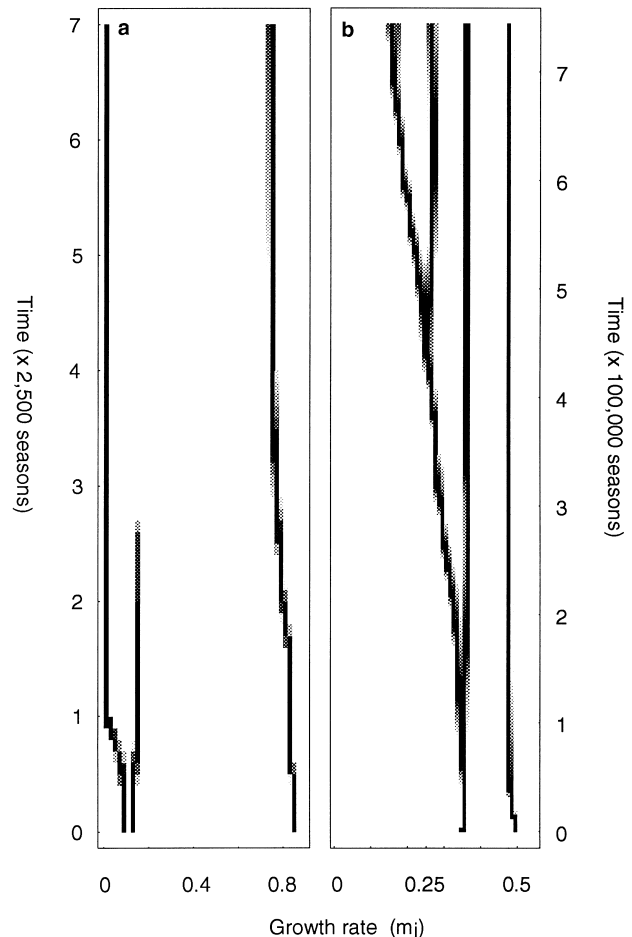


Figure 3 Results of the simulation model. (a) For $\tau=10$, $c=10$, $\omega=1$, $m_{\min}=0.02$, $m_{\max}=0.9$ three types can coexist in ecological time, but at the evolutionary attractor only two coexist. (b) For $\tau=30$, $c=2.2$, $\omega=1$, $m_{\min}=0.01$, $m_{\max}=0.55$ evolution generates biodiversity through the generation of new morphs by adaptive radiation. Note the difference in time scales.

competition becomes more important. An increase in environmental quality also causes an initial increase in the number of types in the evolutionarily stable assemblage, followed by a decrease. Figure 4(b) gives the maximum number of types that can coexist in the evolutionarily stable assemblage, as a function of the environmental quality and the length of the productive season.

DISCUSSION

The biodiversity in our model increases with season length. Since the length of the productive season decreases with latitude, our model predicts an increase in the number of types towards the equator. For a given season length the maximum number of types in a stable assemblage is achieved for intermediate environmental quality, thus the curve of the average number of types against productivity

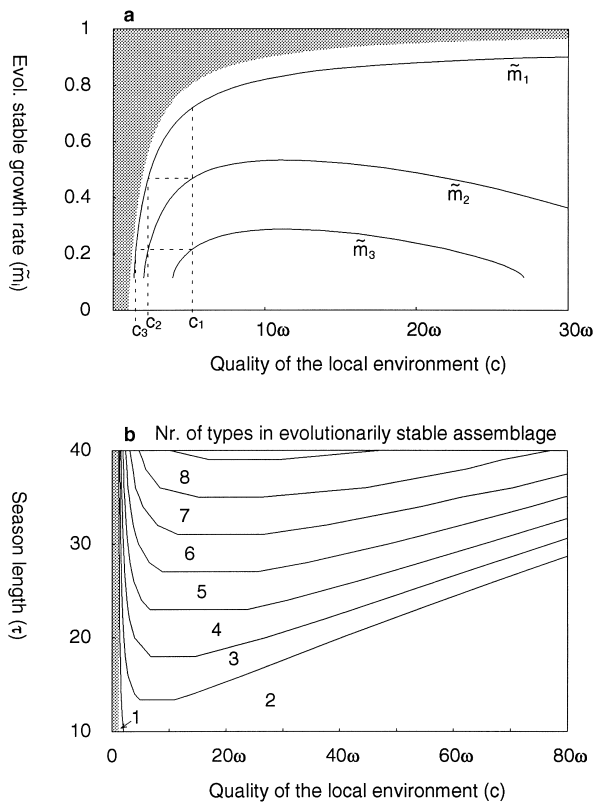


Figure 4 (a) The values of the evolutionarily stable growth rates, \tilde{m}_i , against the quality of the local environment, c (dotted lines illustrate the scaling procedure as outlined in the text). In the grey area no type can persist. (b) The maximum number of types in the evolutionarily stable assemblage.

is humped. These patterns in the biodiversity of types in the stable assemblage show a striking resemblance to patterns in species' diversity. Given that the same selective forces that can create diversity in types can give rise to speciation (Dieckmann & Doebeli 1999), we postulate that our results also apply to diversity in species.

An increase in season length will select types, or species, that are locally more competitive. Because a more competitive type is less fecund, such a type will attain a lower population density. This will leave a larger fraction of patches open for the next best competitor. This argument applies to all types in the assemblage and explains the increase in the number of species in the evolutionarily stable assemblage with season length.

Similarly, we can explain the humped curve for biodiversity against local environmental quality: a richer local environment will generally increase the population density of the most competitive species. For a less competitive type an increase in environmental quality will have two opposed effects: because the local environment is richer, it will produce more seeds. But because a

richer environment will also increase the number of patches occupied by the best competitor, it will decrease the number of effectively available patches. The combined action of these two opposed effects causes an optimum for all types but the best competitors. Because these explanations are independent of the details of the model we can expect these patterns in biodiversity to be robust and to occur in other models. A similar pattern has been observed by Hochberg & Van Baalen (1998) in a coevolutionary predator-prey model. In this model biodiversity is maintained through a combination of a discrete trait space with migration over a productivity gradient.

To keep our model tractable a number of assumptions had to be made. Many of the assumptions can be relaxed without changing the qualitative outcome of the model. For instance, different forms of within patch dynamics can be chosen without changing the outcome drastically, as long as the trade-off between competitive ability and fecundity is maintained. Different within patch dynamics can be analysed using techniques similar to the ones used in this paper, although the mathematics will be more complicated. We also assumed that seeds were distributed according to a Poisson distribution. For many plant species this might not be the case. However, for other seed distributions we expect similar qualitative results, as long as the distribution is sufficiently clustered so that some patches receive no or few seeds (Cohen & Eshel 1976). The clustering affects the relatedness, which is an important factor in models of kin and group selection and models for the evolution of altruism (Frank 1999). Also in our model the selection is partly through relatedness and its associated inclusive fitness.

Our results indicate that patterns in biodiversity result less from a process of assembly, of which the outcome is more or less random, than a process of selection and evolution with a strong deterministic component. If this were true, the biodiversity in locations with the same latitudes and environmental parameters should be similar. In marine ecosystems many environmental conditions, like the amount of solar radiation or surface water temperatures, strongly depend on the latitude. Our model predicts that in this case biodiversity should almost uniquely depend on latitude. The biodiversity of marine prosobranch gastropods in the American coastal waters provides some empirical support for this hypothesis: the number of species at the same latitude on the Atlantic and Pacific coast are remarkably similar (Roy *et al.* 1998). This indicates that biodiversity patterns may be generated by a deterministic evolutionary process driven by the local population dynamics. The outcome of this process will depend on the parameters of the environment it is set in. Geographical variation in environmental parameters can thus lead to patterns in biodiversity, but the mechanism

producing these patterns is natural selection.

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APPENDIX: DESCRIPTION OF THE SIMULATION MODEL

For the simulation model we extended the model for a mutant and resident to a model containing many types by assuming that within a season, the amount of biomass of a type (V_i) within a patch changes according to $dV_i/dt = (m_i - S/c)V_i$ where $S = \sum_{j=1}^n V_j$ is the total amount of biomass in a patch. To calculate the densities we used the variables S and $F_i = V_i/S$, which change as

$$\frac{dS}{dt} = \left(\sum_{i=1}^n m_i F_i - S/c \right) S \quad (6)$$

$$\frac{dF_i}{dt} = F_i \left(m_i - \sum_{j=1}^n m_j F_j \right)$$

The latter equation can be solved: $F_i(K, t) = k_i e^{m_i t} / \sum_{j=1}^n k_j e^{m_j t}$, where k_j is the amount of seeds of type j in a patch (which is assumed to be proportional to the amount of biomass of type j at $t=0$), K is a vector that contains the n non-negative integers k_j . S is approximated by its quasi steady state: $S(K, \tau) \approx c \sum_{i=1}^n m_i F_i(K, \tau)$. Hence the amount of seeds of a type at the end of the season is $T(m_i) V_i(K, \tau)$. The average number of seeds per patch of type i (N_i) in the next season, N'_i , is given by $N'_i = \sum_{\text{all } K} T(m_i) V_i(K, \tau) P(\underline{K} = K)$ where $P(\underline{K} = K)$, the probability that a patch has k_1 seeds of type 1, k_2 seeds of type 2 etc., is multivariate Poisson distributed: $P(\underline{K} = K) = \prod_{j=1}^n e^{-N_j} N_j^{k_j} / k_j!$. These sums were evaluated until P decreased in k_j and had fallen below a threshold. If the expected number of seeds in the total population was less than one it was set to zero, i.e. if $N_i < 1/q$, where $q = 10^8$ is the total number of patches in the population. To describe evolution in our simulation the phenotype space is partitioned into 50 equally sized compartments and every seed can be a mutant in an adjacent compartment with a probability of 5×10^{-11} . To avoid that new mutants were removed as soon as they were produced it was assumed that for a newly produced mutant $N'_i = 1.2/q$.

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