

Slight differences among individuals and the unified neutral theory of biodiversity

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Abstract

The unified neutral theory of biodiversity provides a very simple and counterintuitive explanation of species diversity patterns. By specifying speciation, community size and dispersal, and completely ignoring differences among individual organisms and species, it generates biodiversity patterns that remarkably resemble natural ones. Here I show that adding even slight differences among organisms generates very different patterns and predictions. In large communities with widespread dispersal, heritable differences in viability among individual organisms lead to biodiversity patterns characterised by the overdominance of a single species comprising organisms with relatively high fitness. In communities with local dispersal, the same differences produce rapid community extinction. I conclude that the unified neutral theory is not robust to slight deviations from its most controversial assumption.

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1. Introduction

The unified neutral theory of biodiversity provides a very simple and counterintuitive explanation of species diversity patterns (Hubbell, 2001). By specifying speciation, dispersal and community size, and assuming that individual organisms and species are ecologically identical, it generates species abundance distributions and species-area curves that are remarkably similar to natural ones (see McGill, 2003).

Zhang and Lin (1997) and Yu et al. (1998) criticized a previous version of the theory (Hubbell, 1979; Hubbell and Foster, 1986) on the grounds that relatively small differences in fecundity or mortality among species produced substantial deviations from purely neutral expectations. They found that most species disappeared more rapidly, and communities ended up with fewer species, than in the purely neutral model. Hubbell (2001) devoted the final pages of his book to counterarguing

that limited dispersal indefinitely delays the exclusion of inferior competitors, rendering small fitness differences among species unimportant (see also Hubbell et al., 1999).

I have incorporated slight, heritable differences in viability among individual organisms to computer simulations of the community model used in the unified neutral theory of biodiversity. As expected, this usually results in one species becoming disproportionately abundant and the remaining ones being very rare. As argued by Hubbell (Hubbell et al., 1999; Hubbell, 2001) local dispersal delays the elimination of inferior variants, and so favours diversity in the short run. However, this also results in the steady decline of the average viability of the community and, ultimately, its extinction.

2. Methods

I have modified the basic community model of the unified neutral theory of biodiversity to account for

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deleterious and beneficial mutations. In my simulations space is a torus of cells or sites, each of which can hold a single reproductive individual. Initially every site has an individual with a viability of 1. Every individual produces eight propagules and then dies. Each propagule inherits the viability of its parent and then acquires a number of mutations drawn randomly from a Poisson distribution with mean 1 (Keightley and Eyre-Walker, 1999; Lynch et al., 1999). Most mutations are deleterious and decrease fitness by 5% on average, and the remaining ones are beneficial and increase it by 1% on average (see Keightley and Eyre-Walker, 1999; Lynch et al., 1999; Keightley and Lynch, 2003; Shaw et al., 2003). Both effects have negative exponential distributions (see e.g. Schultz and Lynch, 1997; Orr, 2003). If a beneficial mutation sets viability above 1, this is automatically reset to one. After the occurrence of mutations, the program generates a uniform random number between 0 and 1 for each propagule. A propagule survives if the number is lower than its viability.

In simulations with global dispersal, surviving propagules disperse to randomly selected sites. In simulations with local dispersal, each propagule disperses to a random direction and to a distance drawn randomly from the D2t dispersal kernel of Clark et al. (1999), which combines a Gaussian distribution near parents with a fat tail farther away. To investigate the effects of dispersal I kept $u=1$, and varied p (as in Chave et al., 2002). After dispersal, in each site a propagule is randomly selected among those present and becomes ready for reproduction, and the remaining ones die. Sites with no propagules remain vacant at least until the next time step.

Each time step a certain number of sites are randomly selected, and the individuals present in those sites, if there are any, become new species by means of a purely neutral mutation (as in Hubbell, 2001 and Chave et al., 2002). As the mechanism of speciation is neutral, the organisms of the new species have the same expected viability as those of the species already present. Differences in average viability among species arise exclusively as a result of stochastic variation among individual organisms.

I periodically computed the number and average viability of individuals, the abundance of species and species–area curves. For species–area curves I counted the number of species in contiguous areas, not in sample sites, when dispersal is local (see Chave et al., 2002 for details). After a number of generations these measurements cease to change in a consistent way (otherwise the community goes extinct; see below). I then obtained 10 new measurements sufficiently spread in time to avoid correlation. The results shown correspond to the averages, and sometimes also the standard deviations, of these 10 measurements.

The simulations reproduce the same processes studied by Hubbell (2001; dynamics of a “metacommunity”) and Chave et al. (2002), except for the occurrence of mutations affecting fitness. Without mutations, my results are identical to theirs. These authors have shown that several different algorithms and minor variants of the model produce equivalent results. In their models, in each time step a randomly selected individual dies and the offspring of one of the surviving members of the community takes its place. Thus, individuals vary randomly in their longevity and, as a result, in their lifetime reproduction. In my simulations all adults die in each time step, so generations do not overlap and all individuals have the same lifetime reproductive output. Communities with non-overlapping generations have a larger effective size than communities with overlapping generations (see, e. g., Falconer, 1989). This means that the number of generations to extinction and the relative abundance of species of a community in my model correspond to a community of larger explicit size in the models of Hubbell (2001) and Chave et al. (2002).

With finite fecundity it is possible that communities have fewer individuals than the available space permits, while the unified neutral theory of biodiversity explicitly applies to saturated communities. However, all the results for species abundance patterns and species–area curves I present and discuss below correspond to communities with >99% of space occupied.

For some simulations without mutation I used the algorithms for species–area curves and species abundance distributions detailed in Hubbell (2001, p. 163–164, 289–290). I verified that these algorithms produce the same results as the procedure above (without mutation) for a sample of the cases.

In the Results, I report on the outcomes of simulations using a limited range of values of the relevant parameters. However, the genetical studies that I cite in the Discussion offer or review abundant evidence, based on computer simulation and mathematical models, that similar results hold for most, if not all, reasonable values of those parameters, as well as for more complex systems involving sexual reproduction, recombination, dominance or epistasis. To illustrate the effect of mutations on community extinction I used a ratio of beneficial to deleterious mutation of 0.1. To illustrate effects on species abundance patterns I used a ratio of 0.3, which yields exceedingly long expected extinction times for the communities analysed.

3. Results

Small communities or communities with short dispersal distances rapidly go extinct, while large communities with widespread dispersal are relatively safe (Figs. 1 and 2). Communities that are virtually safe

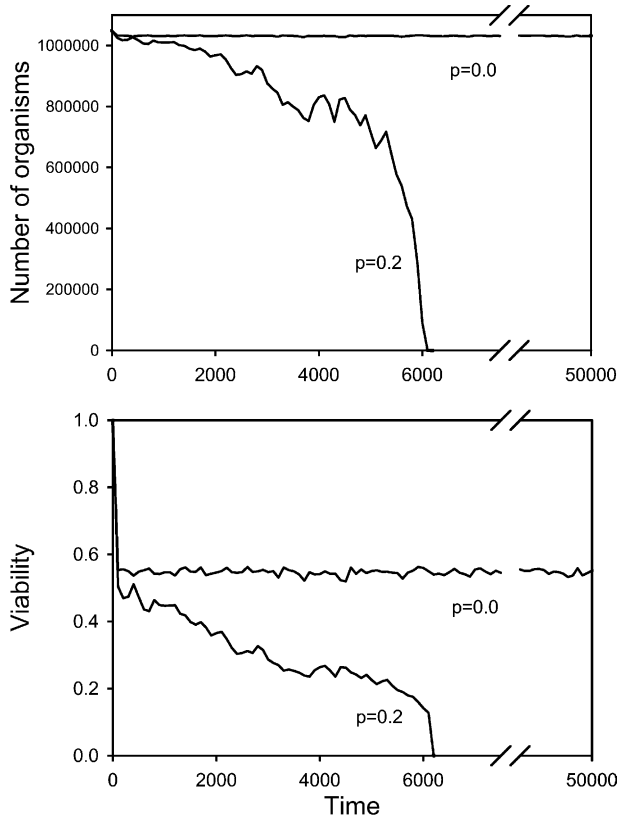


Fig. 1. Total number of organisms and mean viability through time (in number of generations) in two sample communities, one with global dispersal ($p=0.0$) and the other with widespread but finite dispersal ($p=0.2$). The former has a very long expected time to extinction, while the latter rapidly goes extinct. Both communities have 1,048,576 sites, and a ratio of beneficial to deleterious mutation rate of 0.1.

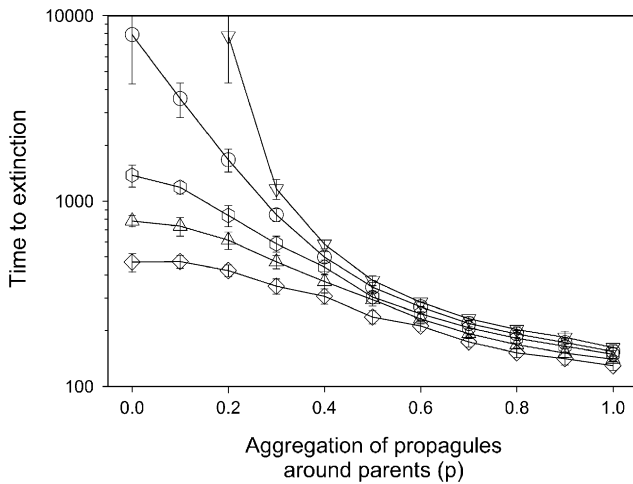


Fig. 2. Time (generations) to extinction of model communities. Larger values of p represent more local dispersal around parents (when $p=0$ dispersal is global). Lines represent communities of different sizes: 1,048,576 (inverted triangles), 262,144 (circles), 65,536 (hexagons), 16,384 (upright triangles) and 4096 individuals (diamonds). I represent the mean and standard deviation of 10 samples for each kind community. The ratio of beneficial to deleterious mutation rate is 0.1.

from extinction display species abundance patterns and species–area curves that are very different from those generated by the unified neutral theory (Fig. 3). One species is disproportionately abundant and the remaining ones very rare, leading to species rank–abundance curves that have a characteristic L shape. Species–area curves are concave (J-like), as most species are so rare that they are detected only when inspecting large areas. Larger communities show larger deviations from the strictly neutral expectation (Fig. 3). Holding the number of new species per generation constant, species–area curves become more J-like, rank-abundance curves more L-like, and the number of species per sample smaller in communities of larger size (Fig. 3).

4. Discussion

Communities of unequal organisms display species abundance patterns that are very different from those generated by the unified neutral theory. One species, which usually includes the fittest class of organisms, is overly dominant, and the remaining ones are very rare (see also Zhang and Lin, 1987; Yu et al., 1998; Hubbell, 2001, p. 337). This parallels the patterns found for allele frequencies in theoretical populations subjected to selection (Ewens, 1979; Charlesworth et al., 1993; Gillespie, 2001; Gordo et al., 2002). In larger communities, selection is more efficient in keeping less fit variants in low numbers, and overdominance is more extreme. Communities in which inferior competitors are not readily eliminated may resemble purely neutral communities in the short run, but they inevitably go extinct.

Natural selection tends to eliminate less viable variants. However, the fate of slightly different variants may depend more on demographic stochasticity (drift) than on selection, especially in small populations. As a result, mildly deleterious mutations may accumulate over time, steadily reducing the average absolute fitness of populations. Viability may get so low that reproduction cannot balance mortality and populations go extinct (Figs. 1 and 2; see Lynch et al., 1993, 1995a, b; Lande, 1994 for theoretical outlooks; and Fry, 2001; Zeyl et al., 2001; Rowe and Beebe, 2003 for empirical evidence in the laboratory and in the wild). The assumption of constant community size in the unified neutral theory of biodiversity holds only when inferior competitors are readily eliminated from the community.

With a substantial rate of beneficial mutation, very large communities with widespread dispersal are virtually safe from extinction by mutation accumulation. In these communities, less fit variants are rapidly eliminated and beneficial mutations occasionally spread across the community enhancing its fitness. Local

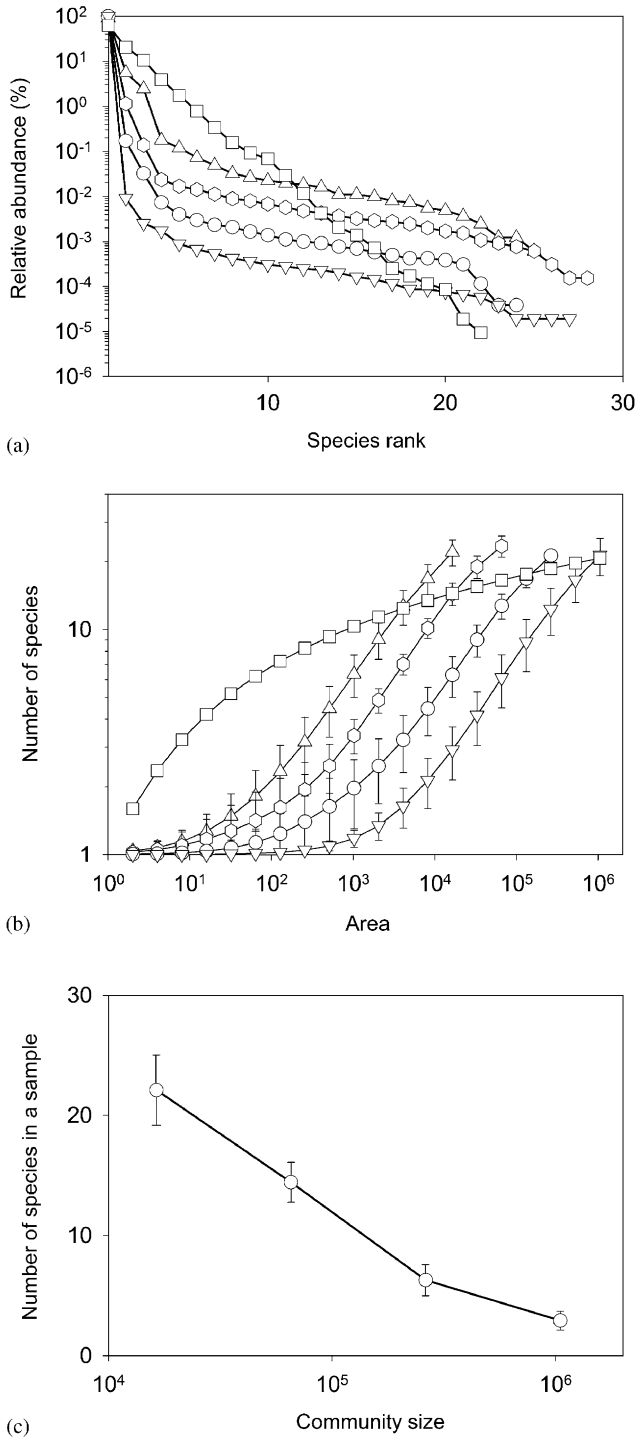


Fig. 3. Biodiversity patterns of model communities. (a) Species rank-abundance curves. Communities with fitness differences have sizes (J_M) of 1,04,8576 (inverted triangles), 262,144 (circles), 65,536 (hexagons) and 16,384 individuals (upright triangles), and speciation rates (v , measured as number of new species per individual and time step) that satisfy $J_M v = 5$ species/generation. The ratio of beneficial to deleterious mutation rate is 0.3. For the unified neutral theory the curve represents every community that satisfies $J_M v = 0.75$ species/generation, which yields a number of species per sample of 16,384 individuals comparable to those of the above communities. In all cases dispersal is global. (b) Species–area curves. Parameters and symbols as in (a). I represent the mean and standard deviation of 10 samples from each nearly neutral community. (c) Number of species in a sample of 16,384 individuals in nearly neutral communities differing in total number of individuals. Parameters as in (a) and (b). I represent the mean and standard deviation of 10 samples from each community.

sample of individuals (Hubbell, 2001). The number θ equals $2J_M v$, J_M being the size of the community and v the speciation rate per individual and generation. Thus, all communities that have the same absolute number of new species appearing per generation ($J_M v$) have exactly the same above properties. This is not true of communities with fitness differences. Holding θ constant, under larger values of J_M species–area curves become more J-like, rank-abundance curves more L-like, and the number of species per sample smaller (see also Ewens, 1979).

I conclude that the unified neutral theory of biodiversity is not robust to even slight deviations from its assumption of equality among individual organisms. Under low community size, very slight fitness differences among organisms, low reproductive output, or short distance dispersal, communities go rapidly extinct. Only communities where inferior competitors are consistently kept in low numbers are relatively safe from extinction. These communities, however, display biodiversity patterns that are very different from those of the unified neutral theory.

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dispersal accelerates extinction, as it lowers both the community effective size (Higgins and Lynch, 2001; Kawata, 2001) and the effective reproductive output of individuals (as a larger fraction of their offspring are “wasted” by attempting to settle in the same sites).

In the unified neutral theory, a single “fundamental biodiversity number” θ generates rank-abundance and species–area curves, and the number of species in a given

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