A unified theory of biogeography and relative species abundance and its application to tropical rain forests and coral reefs

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Abstract. Theories of island biogeography and of relative species abundance are of central importance in biogeography and community ecology, yet these two bodies of theory heretofore have been largely unconnected. Incorporating speciation into the theory of island biogeography unexpectedly results in unification of these two theories. The unified theory predicts the existence of a fundamental biodiversity number θ that controls not only species richness, but also relative species abundance in the source area metacommunity at equilibrium between speciation and extinction. With additional parameters for island size and migration rate, the theory also predicts relative species abundance on islands or local regions of continuous landscapes. Application of the theory to the biogeography and biodiversity of communities of tropical trees and reef-building corals are discussed. One important result is that only relatively modest migration rates are sufficient to dynamically couple the regional metacommunity and stabilize community structure on large spatiotemporal scales. Thus, regional, long-term compositional stasis in tropical rain forests and coral reefs can arise just as easily from the stabilizing effect of large numbers as from niche-assembly rules that limit species membership in communities. Because of the higher intrinsic vagility of corals, the theory predicts greater regional similarity in coral reef communities than in tropical tree communities.

Introduction

Biogeographers and community ecologists typically work on very different spatial and temporal scales, and therefore it is hardly surprising that their theories for how biotas and ecological communities are assembled should differ. Ecologists tend to focus on small-scale processes shaping the interactions of individuals and populations. They tend to be impressed by the strength and importance of species interactions and of niche differences in stabilizing species assemblages in particular locations. Biogeographers, on the other hand, focus on much larger scale processes and ask questions about migration and range and speciation and extinction in space and time. One might label these two perspectives of the organization of ecological communities as the "niche assembly" and "dispersal assembly" views, although these terms do not adequately capture the large differences in viewpoint that exist within each perspective. For example, theories in vicariance biogeography tend to downplay the role of dispersal in assembling regional biotas compared to theories in pan-biogeography.

The equilibrium theory of island biogeography (MacArthur and Wilson 1963, 1967) was a bold attempt to link these two very different scales and perspectives. MacArthur and Wilson proposed that biotas inhabiting islands or insular habitats are in diversity equilibrium but not in taxonomic equilibrium. They suggested that local communities experience a continual turnover of species through immigration and local extinction of species drawn from a large source area or metacommunity. The equilibrium diversity on isolated islands was expected to be lower than on a similar-sized piece of the continuous mainland primarily because of a reduction in immigration rates due to isolation and increased extinction rates due to smaller island population sizes. Various embellishments were later added to the theory. For example, Brown and Brown (1977) suggested that immigration would interact with extinction to produce a "rescue effect", further reducing local extinction rates in continuous landscapes.

However, for all its attempts to bridge the conceptual gulf between ecology and biogeography, the theory of island biogeography departs fundamentally from classical niche-assembly theory. Gone are niche differences among species. Species in the theory are treated as identical, subject to the same birth and death processes and the same probabilities of immigration and extinction. If species are not identical, then the theory's simplification of the dynamics of island communities to enumerating species irrespective of taxa logically does not work. Thus, the theory is far closer to theories of pure dispersal assembly than to the niche assembly theories of classical ecology, which ironically, MacArthur also championed as

the leading ecological theorist of his day (MacArthur 1972). Apart from whether one accepts the radical assumption of identical species, the theory of island biogeography is also conceptually incomplete in a number of important regards. From a biogeographer's perspective, it is incomplete because it embodies no mechanism of speciation. Although species can appear and disappear from islands or habitats in the theory, this is a migration- and local extinction-driven phenomenon; no new species are allowed to originate in islands or in the source area.

From an ecologist's perspective, the theory is incomplete in large part because it does not predict the abundances of species, only species richness. Relative abundance theory is briefly touched upon in MacArthur and Wilson's (1967) monograph in relation to the species-area relationship. However, the expected equilibrium distribution of relative species abundance on islands was not derived from the first principles of the theory. Just a few years earlier, MacArthur (1957, 1960) published two papers on relative species abundance, but these papers were steeped in niche-assembly theory and did not readily lend themselves to a dispersal assembly theory. Later, May (1975) examined more fully the consequences of relative species abundance for species-area relationships, assuming that relative abundances were log-normally distributed (Preston 1948, 1962). However, this was a static sampling analysis, not a dynamical theory based on fundamental birth, death, and migration processes. Indeed, most of the existing models of relative species abundance are empirical statistical fits to observed distributions of abundance (Motomura 1932; Fisher et al. 1943; Preston 1948, 1962), or are based on static niche-assembly hypotheses (MacArthur 1957, 1960; Sugihara 1980) and are not grounded in a dynamical theory that can be related directly to the dynamical theory of island biogeography. The exceptions to this generalization are the theories of Casewell (1976), who proposed neutral models of community organization based on analogs in population genetics, Chesson and Warner (1981), who proposed that species abundances were determined by stochastic, frequency-dependent recruitment fluctuations, and Hughes (1984), a benthic ecologist who proposed a model similar to my own stochastic forest dynamics model (Hubbell 1979), which was a less general version of the theory discussed here.

A unified theory of island biogeography and relative species abundance

In a forthcoming monograph, I attempt to formally generalize and unify the theories of island biogeography and relative species abundance into a single, dynamical theory (Hubbell 1997). This theory is a direct generalization of the equilibrium theory of island biogeography. It rests on a key first principle, namely that the interspecific dynamics of ecological communities are a stochastic zero-sum game. This assumption is reasonable and appropriate for all communities of trophically similar, competing species in which individuals saturate all limiting resources. This includes space-limited communities such as closed-canopy forests, rocky intertidal communities, or communities

of reef-building corals. It is also appropriate for communities limited by other resources, with the proviso that all limiting resources are utilized to saturation. By *saturated*, I mean that no births or immigrants in a community are allowed until deaths create vacancies. The theory explicitly and analytically describes the stochastic birth, death, and migration of competing species obeying this zero-sum game. The theory can then be applied to any arbitrary biogeographic situation, from the classical island-mainland problem of the theory of island biogeography, to a metacommunity fragmented over an archipelago of islands, and finally to the continuous landscape case of fully contiguous local communities (Hubbell 1995, 1997).

The theory further generalizes island biogeography theory by explicitly including a process of speciation. Given the lack of any generally accepted, quantitative genetical or ecological theory of speciation, I have chosen to model speciation in the theory by the simplest possible mechanism. New species arise in the theory like rare point mutations, and they may spread and become more abundant or, more likely, die out quickly. New species can arise anywhere: on the mainland, on islands, or in an archipelago of islands or habitats. Corals and rain forest trees almost certainly have more complicated, sometimes "reticulate" evolution (e.g., Veron 1995). Many species probably arise through the vicariant allopatric subdivision of ancestral species and never pass through a period of absolute rarity at origination. It turns out that allopatric speciation does not alter the fundamental theory, but it does affect equilibrium metacommunity biodiversity (Hubbell 1997). Here I discuss only the predictions of the simplest possible model of speciation for biogeographical patterns of diversity and community organization.

The unified theory of island biogeography and relative species abundance is a conceptual advance over either theory taken separately. In current theories of relative species abundance, the number of species in the community is a free parameter that cannot be derived from first principles (Motomura 1932; MacArthur 1957; 1960; Fisher et al. 1943; Preston 1948, 1962; Cohen 1968; Sugihara 1980). In the unified theory, the equilibrium number of species is a prediction as in the theory of island biogeography, but so also is relative species abundance. MacArthur and Wilson devoted a large section of their 1967 monograph to discussing the relationship between island population size and risk of extinction. Without a theory of speciation and relative species abundance, however, they were unable to make headway on many other issues of central importance to community ecology and conservation biology, including expected abundances of species on islands and in the metacommunity and their variances, species incidence functions and times to extinction and recolonization, patterns of island and metacommunity dominance and diversity, and species-individual and species-area relationships. Much progress has been made on theory for a number of these problems individually (e.g., May 1975; Casewell 1976; Coleman 1981; Quinn and Hastings 1987; Casewell and Cohen 1991; Hanski and Gilpin 1997; Durrett and Levin 1996). Now all of these problems are analytically tractable in the unified theory (Hubbell 1997).

A synopsis of the theory

I divide the problem into two scales: local community dynamics and regional metacommunity dynamics. First consider a local or island community saturated with individuals of all competing species, such that all space or other limiting resource is utilized, and the dynamics are a zero-sum game. Define the scale of the local community as the maximum patch size on which dispersal limitation can be ignored. Now kill an individual at random in the community, and replace it with another individual. Let the replacement individual be drawn from the local community at random with probability $1 - m$, and be an immigrant from the metacommunity with probability m. Scale time so that one death occurs per unit time. Let parameter J be the size of the local community (total number of individuals of all species. Let N_i be the abundance of the ith species. Let P_i be the relative abundance of the ith species in the source area or metacommunity. Then the probability that the ith species will lose an individual, gain an individual, or stay the same abundance in the next time unit is given by the equations in Fig. 1.

It is straightforward to explain these equations in words. For example, the first equation gives the probability for the ith species to decline in abundance by one individual. For this to happen, a death must occur in the ith species. N_i/J_i, and the birth must be in some other species. The first probability inside the brackets is that of an immigration event of some species other than the ith: $m(1 - P_i)$. The second probability is that of having no immigration event and a local birth in a species other than the ith: $(1 - m)(J - N_i)/(J - 1)$.

As in island biogeography theory, a species can immigrate or become extinct on an island or in a local community. The probability that the ith species will be at any abundance from 0 (extinct) to J (monodominant) in the local community can be found from the equilibrium eigenvector for the equations in Fig. 1 (Hubbell 1997). The eigenvector gives the complete probability density function for the ith species in the local community. The expected local abundance of the ith species depends only on local community size J and the source area relative abundance of the ith species P_i: $E\{N_i\} = JP_i$, but the variance also depends on the immigration rate m. Figure 2 shows how the local abundance of the ith species depends on its source area abundance P_i. When the species is very abundant in the source area, it is also expected to be very

Fig. 2. Equilibrium probability density functions for the ith species in a local community of size $J = 64$, for various values of metacommunity relative abundance P_i. The immigration probability in this example was set at $m = 0.05$

abundant in the local community, and vice versa. The behavior of the eigenvector is more complex when the immigration rate m is varied (Fig. 3). When the migration rate is large, the abundance of the ith species is strongly unimodal about its mean JP_i. When the immigration rate is small, however, the probability density function becomes U-shaped, Then the ith species spends most of its time either locally extinct or monodominant, and the proportion of time extinct or monodominant is dictated by its source area abundance P_i (Fig. 3). The importance of this result will become more apparent when the dynamical coupling of local communities to the metacommunity by dispersal is discussed.

I now consider large-scale metacommunity dynamics. In the original theory of island biogeography the metacommunity was treated as a permanent pool of potential

$$\Pr\{N_i - 1 | N_i\} = \frac{N_i}{J}\left[m(1 - P_i) + (1 - m)\left(\frac{J - N_i}{J - 1}\right)\right]$$

$$\Pr\{N_i | N_i\} = \frac{N_i}{J}\left[mP_i + (1 - m)\left(\frac{N_i - 1}{J - 1}\right)\right] + \left(\frac{J - N_i}{J}\right)\left[m(1 - P_i) + (1 - m)\left(\frac{J - N_i - 1}{J - 1}\right)\right]$$

$$\Pr\{N_i + 1 | N_i\} = \left(\frac{J - N_i}{J}\right)\left[mP_i + (1 - m)\left(\frac{N_i}{J - 1}\right)\right]$$

Fig. 1. Transition probabilities for a single time step for the ith species with abundance N_i in the local community, and relative abundance P_i in the source metacommunity
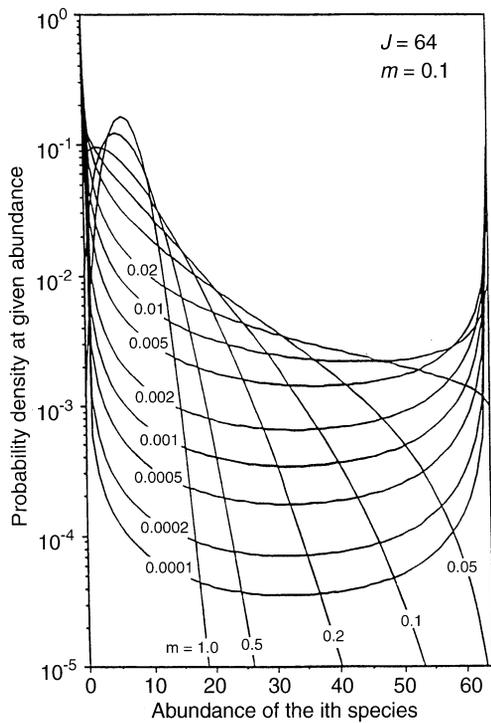
Fig. 3. Equilibrium probability density functions for the ith species in a local community of size $J = 64$, for various values of the probability of immigration, m. The metacommunity abundance P_i is 0.1 in this example. The distribution becomes U-shaped for small m

immigrant species to islands. In reality, all species ultimately become extinct in the source area, though usually at slower rates than on islands because of larger source area population sizes. In the source metacommunity speciation is analogous to immigration on islands. A steady-state species richness and relative species abundance will arise in the source metacommunity at equilibrium between speciation and extinction.

To solve for the equilibrium in the source metacommunity, we can take advantage of an analytical strategy developed by Ewens (1972) and Karlin and MacGregor (1972) for an analogous problem in population genetics. Let J_M be the size of the source metacommunity (total number of individuals of all species) and v be the speciation rate. The strategy is to calculate the unconditional equilibrium probability of every possible configuration of relative species abundance in a sample of J individuals drawn randomly from the metacommunity (Ewens 1972; Hubbell 1997). Let $\theta = 2J_M v$. Then the probability of obtaining S species with $n_1, n_2, \ldots, n_S$ individuals, respectively, where $J = \Sigma n_i$, is:

$$\Pr\{S, n_1, n_2, \ldots, n_S\} = \frac{J!\theta^S}{1^{\phi_1} 2^{\phi_2} \ldots J^{\phi_J} \phi_1! \phi_2! \ldots \phi_J! \prod_{k=1}^{J} (\theta + k - 1)},$$

where ϕ_i is the number of species that have i individuals in the sample of size J. With no loss in generality, rank order species in each configuration from common-nest to rarest. Then the expected abundance r_i of the ith ranked species

in the equilibrium rank-ordered relative abundance distribution for a random sample of size J individuals from the metacommunity is:

$$\mathrm{E}\{r_i | J\} = \sum_{k=1}^{C} r_i(k) \cdot \Pr\{S, r_1, r_2, \ldots, r_S, 0, 0, \ldots, 0\}_k,$$

where C is the total number of configurations, $r_i(k)$ is the abundance of the ith ranked species in the kth configuration, and $Pr(S, r_1, r_2, \ldots, r_S, 0, 0, \ldots, 0)_k$ is the probability of the kth configuration. Analytical details are given in Hubbell (1997). The dynamics of the much larger source metacommunity are negligibly slow relative to the dynamics of the local or island community, so we can treat metacommunity relative species abundances as a fixed marginal distribution; and $P_i = r_i$ of the source area distribution. Thus, we can henceforth conveniently dispense with the only species-specific parameter in the theory, P_i (Hubbell 1997). The theory then simplifies to just three parameters: the number θ, island or local community size J, and migration rate m. The parameters of metacommunity size J_M and speciation rate v, always appear combined into the single composite parameter θ.

A fundamental biodiversity number

In the unified theory, θ is a fundamental dimensionless number that controls both the steady-state species richness and the distribution of relative species abundance in the source metacommunity (Fig. 4). When θ is small (e.g. 0.1) the expected dominance-diversity curve is steep and geometric-like, with high dominance. However, as θ becomes larger the expected dominance-diversity distributions become more S-shaped, as is observed in many species-rich communities. Eventually, in the limit when $\theta \to \infty$, the dominance-diversity curve becomes a perfectly horizontal line (infinite diversity), such that every individual sampled represents a new and different species, regardless of how large a sample is taken. At the other extreme, when $\theta = 0$, the distribution collapses to a single monodominant species everywhere in the metacommunity. The curves in Fig. 4 are remarkably similar to the dominance-diversity curves observed over a latitudinally broad range of closed canopy tree communities (Fig. 5). The distribution of metacommunity relative species abundances is the log-series (Watterson 1974; Hubbell 1997) and the fundamental biodiversity number θ turns out to be identical to Fisher's α, which is a parameter of the log-series. Fisher's α is a widely used measure of biodiversity introduced by Fisher et al. (1943) more than 50 years ago.

The fit of the expected distribution to observed relative abundance data is often remarkably precise, at least for closed-canopy tree communities. Such fits are illustrated in Fig. 6 for two tropical forest tree communities. The top panel gives the dominance-diversity curve for trees > 10 cm dbh in a 50 ha plot of moist tropical forest on Barro Colorado Island (BCI), Panama (Hubbell et al. unpublished). The bottom panel is the corresponding curve from a 50 ha plot in lowland mixed dipterocarp
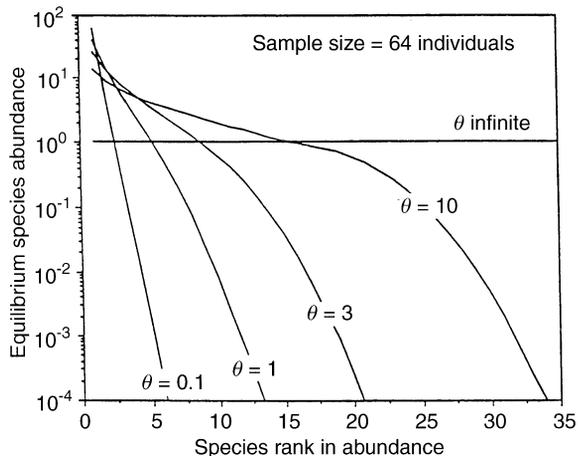
Fig. 4. Expected metacommunity dominance-diversity distributions for a random sample of 64 individuals from the metacommunity, for various values of the fundamental biodiversity number θ
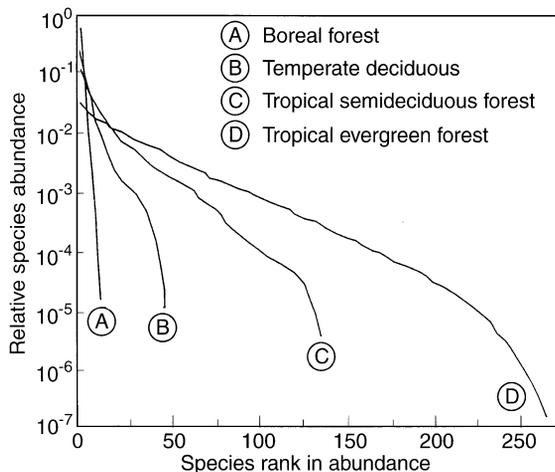
Fig. 5. Dominance-diversity distributions for four closed-canopy tree communities spanning a large latitudinal gradient, from boreal forest to equatorial Amazonian forest, after Hubbell (1997)

Fig. 6. Dominance-diversity distributions for tree species in the 50 ha plots on Barro Colorado Island (BCI), Panama, and at Pasoh Forest Reserve, Negeri Semilan, Malaysia. The *heavy line* is the observed rank abundance distribution. The expected metacommunity log-series are shown for $\theta = 50$ (BCI) and $\theta = 180$ (Pasoh) and are the diagonal lines continuing past the end of the observed distributions. Note the departure of the metacommunity distribution from the observed distribution for rare species. However, when local community dispersal limitation is added ($m < 1$), the unified theory fits the observed distributions almost exactly in each case

tropical forest in Malaysia (Pasoh Forest Reserve), which is two and a half times richer in species (Manokaran et al. 1992). The diagonal line extending downward to the right is the expected metacommunity log-series distribution for best-fit θ values of 50 for BCI and 180 for Pasoh, respectively.

However, the expected relative abundance distribution for a local community is not the log-series and therefore not the same as a random sample of size J from the metacommunity. The local distribution deviates from the log-series especially for rare species. Nor is the local distribution precisely log-normal; it is a new distribution that might be aptly named the *zero-sum multinomial* distribution. This new distribution arises because of an interaction between dispersal limitation and local extinction. This needs some explanation.

Preston (1948, 1962) criticized Fisher's log-series because it predicts that the rarest species will be the most frequent, whereas Preston's data on relative species abundance indicated that species of intermediate abundance are the most frequent. Preston plotted relative abundance data in doubling abundance classes. When species are counted in abundance classes of 1, 2–3, 4–7, 8–15, et cetera, there is almost always a mode at some intermediate abundance class. The unified theory demonstrates that Fisher and Preston were both correct, but on different spatiotemporal scales. Preston had no theoretical explanation for the interior mode of the relative abundance distribution. The unified theory's explanation is that rare species in local communities or islands are more extinction-prone (Hubbell 1997). Frequent local extinction of rare species reduces their local steady-state frequency and abundance below their random-sample expectations from the metacommunity log-series. On islands rare species are too rare and common species are too common.

The effect of dispersal limitation (small m) on the equilibrium distribution of relative species abundance on an island or local community is shown in Fig. 7. At infinite dispersal ($m = 1$), the local community is not isolated form the metacommunity. In this limiting case, the local relative abundance distribution will be a random sample of the
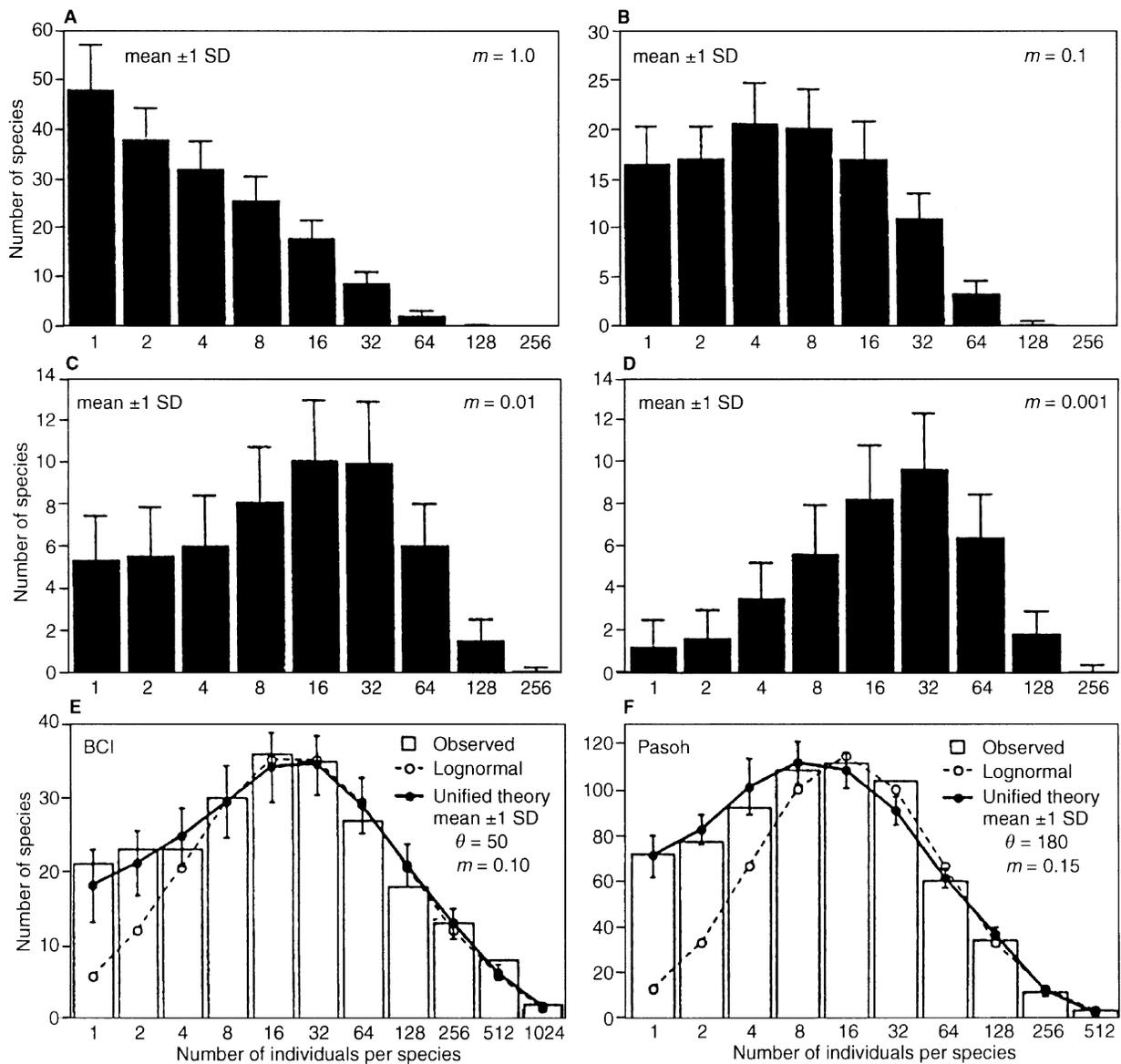
Fig. 7A–F. The effect of dispersal limitation (isolation) on the expected distribution of relative species abundance in a model local community or island, and in the 50 ha BCI and Pasoh forest plots, according to the unified theory. Relative abundance distributions are plotted by doubling classes of abundance, following the method of Preston (1948). In all panels the error bars represent ± 1 standard deviation. **A–D** model community of $J = 1600$ individuals and $\theta = 50$. **A** no dispersal limitation ($m = 1$). This is the distribution of relative species abundance expected in a random sample of 1600 individuals from the metacommunity log-series. **B** Relatively low local community isolation and dispersal limitation ($m = 0.1$).

C Moderate isolation and dispersal limitation ($m = 0.01$). **D** Severe isolation and dispersal limitation ($m = 0.001$). As m decreases rare species become rarer and less frequent, and common species become commoner in the local community or island, resulting in a rightward shift of the mode of the distribution. **E** Preston-type plot of relative species abundance for three species > 10 cm dbh in the BCI plot, compared with expectations from the log-normal and from the unified theory for $\theta = 50$ and $m = 0.10$. **F** Preston-type plot of relative species abundance for tree species > 10 cm dbh in the Pasoh plot, compared with expectations from the log-normal and from the unified theory for $\theta = 180$ and $m = 0.15$

metacommunity log-series, and singleton species will be the most frequent (Fig. 7A). However, as m becomes smaller, the island or local community becomes progressively more isolated, and the shape of the relative abundance distribution changes (Fig. 7B–D). Rare species become ever rarer and common species become ever more common. The unified theory thus predicts that the shape of the relative species abundance distribution will be a function of m. These changes in shape enable one to estimate parameter

m and thereby quantify the average dispersal limitation and degree of isolation affecting a given local community or island. The estimated value of m for the BCI plot is 0.10, or that 90% of the trees in the plot are estimated to have been locally germinated ("births"), and 10% were immigrants. This is a reasonable number for m given that 10% of the area of the plot lies within 17 m of the outer perimeter. This estimate for the Pasoh plot is slightly higher: 0.15. The main canopy at Pasoh is twice as high

than at BCI (50 m vs. 25 m), which may mean that seeds at Pasoh are dispersed farther. Once dispersal limitation is factored in, the expected equilibrium relative abundance distributions fit the observed distributions almost exactly (Figs. 6, 7).

The unified theory also asserts that the reduction of species richness on islands predicted by island biogeography theory will always be accompanied by an increase in the variance of relative species abundance, and therefore by an increase in apparent dominance. This effect is predicted by the fundamental biodiversity number θ in combination with restricted immigration ($m < 1$). As equilibrium species richness declines, the mean and variance in abundance of the remaining species both increase relative to the metacommunity. This predicted effect has been documented in the tree communities on several small islands in the Pearl Archipelago off the south coast of Panama (Hubbell 1995). These islands were attached to the mainland during the last glacial maximum by a now-drowned coastal plain (Fig. 8).
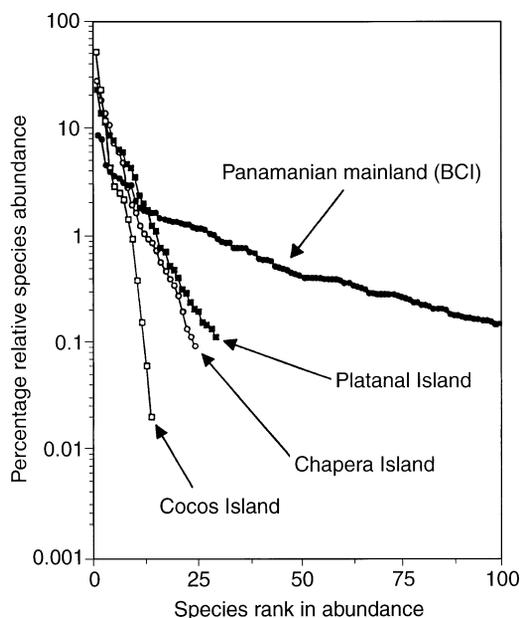
Fig. 8. The dominance-diversity distributions for the tree communities on Chapera, Cocos, and Platanal Islands in the Pearl Archipelago in the Bay of Panama. During the last glacial maximum, these islands were hills surrounded by a broad coastal plain attached to the mainland. The mainland comparison is the dominance-diversity curve for the BCI forest (the BCI curve is truncated at 100 species so that the island patterns can be better revealed in the figure). Distributions are based on counts of trees > 10 cm dbh. Assuming equilibrium has been reached and a source metacommunity exists on the mainland similar to that for BCI, one can estimate the immigration probabilities for each island. These estimates range from a low of 6 in 10 000 births for Cocos Island to a high of 7 in 1000 births for Platanal Island. Cocos, the smallest and most remote island, had the steepest dominance-diversity curve and the fewest species. Platanal, the next smallest island, nevertheless had the greatest species richness and the shallowest dominance-diversity curve. The proximity of Platanal Island to Rey Island, the largest of the islands in the archipelago, may explain Platanal's higher diversity. Chapera, the largest of the three islands but also fairly remote from potential source areas, had intermediate tree species richness and dominance-diversity, data courtesy of S. J. Wright

Preston postulated a fixed ratio of the total number of individuals in the community J to the abundance of the rarest species, which he called his canonical hypothesis (Preston 1962; MacArthur and Wilson 1967). The observed and predicted local community relative abundance distributions in Figs. 6 and 7 are not canonical lognormals *sensu* Preston (1962) and Sugihara (1980), nor indeed are they log-normal. The unified theory predicts an eventual breakdown of the apparent canonical relationship as sample size increases because of the long tail of very rare species in the metacommunity log-series (Hubbell 1995, 1996b). If the distribution were canonical, then in principle one should be able to increase sample sizes sufficiently until the last added and rarest species has abundance > 1. However, in practice this never happens in real samples; the abundance of the rarest species observed almost invariably stays "locked" at 1, irrespective of sample size. The rarest species become ever rarer relative to common species in a seemingly endless regression as sample size increases. Therefore, no fixed ratio of J to the abundance of the rarest species exists.

Local species-area relationships

MacArthur and Wilson (1967) noted in their monograph that large landscapes are essentially always biotically saturated with individuals of a specified metacommunity or taxon, so that $J_M = \rho A_M$, where A_M is the size of the region occupied by the metacommunity, and ρ is the density of organisms. In this case the fundamental biodiversity number θ can also be rewritten as a simple linear function of area and density of organisms:

$$\theta = 2\rho A_M v.$$

Thus, the unified theory of biogeography and relative species abundance asserts that on macroecological scales, to a first approximation, one need only specify the area of the biogeographic region, the density of organisms, and the speciation rate, to predict the equilibrium species richness and relative species abundances in the metacommunity or taxon. Note that this equation also relates biodiversity to landscape productivity insofar as the density of organisms per unit area ρ measures productivity.

The relationship between θ and area implies that a function of θ exists which specifies the species-area relationship. If dispersal is infinite ($m = 1$), then the unified theory makes a simple prediction for the cumulative species-individuals curve. The expected number of species S in metacommunity area A_M is given by:

$$\mathrm{E}\{S\} = \frac{\theta}{\theta} + \frac{\theta}{\theta + 1} + \frac{\theta}{\theta + 2} + \cdots + \frac{\theta}{\theta + J_M - 1}.$$

where $J_M = \rho A_M$ is the size of the metacommunity. This expectation was derived by Ewens (1972) for the problem of sampling selectively neutral alleles in the infinite allele case, and is identical to the case for zero-sum community dynamics. Figure 9 illustrates the expected species-individuals curves for various values of θ. Note that the infinite series $\sum_{i=1}^{\infty} \frac{\theta}{\theta + i - 1}$ diverges as $J_M \to \infty$. This is perfectly all right because an infinite number of species
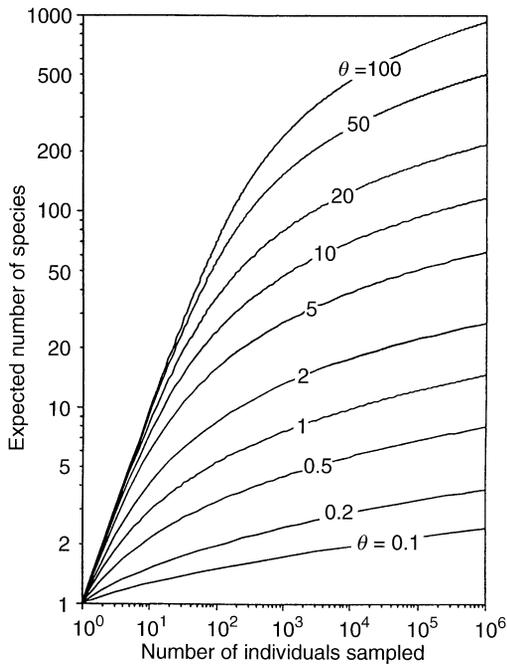
Fig. 9. Expected species-individual curves for values of the fundamental biodiversity number θ ranging over 3 orders of magnitude from 0.1 to 100. Note the log scale on the individuals axis. These are expectations for a random sample of individuals from the metacommunity (no dispersal limitation) and are generally not the curves that would be observed in a local community

Fig. 10. Species-individuals curve for 13 species of the genus *Ficus* in the 50 ha BCI plot. The expected curve is for a maximum-likelihood θ value of 2.9. The error bars are ± 1 standard deviation of 10 random samplings of *Ficus* trees in the plot. The metacommunity distribution fits this genus well probably because figs are very good dispersers

can be counted among an infinite number of individuals. In the real world, J_M is finite (but very large), so there can only be a finite number of possible species. Note also, however, that because $\lim \theta/\theta + J_M - 1 = 0$, successively rarer species are added at an ever decreasing rate as the number of individuals increases. Once parameter θ has been fitted, the total number of species expected in a metacommunity of known size J_M can be calculated.

Figure 10 shows the distribution fitted to the species-individuals curve for the highly dispersive, species-rich genus *Ficus* in the BCI plot. However, in general the equation will seldom fit observed species-individuals curves well because it assumes a completely random sample of individuals from the metacommunity, which is never possible, or a sample from a local community which is not isolated from the metacommunity, which is never encountered. All real organisms in real communities are dispersal-limited on some spatial scale. In most cases, observed species-individuals curves rise more slowly than the metacommunity species-individuals curve predicts. Fortunately, however, the dispersal-limited, real-world species-individuals curve and species-area curve can still be found analytically, but there is no longer a simple and direct formula. This is because, as we have seen, when there is dispersal limitation, θ no longer completely determines local community species richness and relative abundance. The dispersal parameter m now becomes important, as well as local community size J.

Assuming m, J, and θ are known or can be reasonably estimated, then the species-area curve can be found by a two-step procedure: First calculate the expected abund-

ances of each species in the local community from the equilibrium eigenvector for the equations of zero-sum dynamics (Fig. 1). Second, once the expected local abundances of all species are known, calculate the expected species-area curve from Coleman (1981), as follows: let S be the total number of species in the entire area, in which there are N_i individuals of the ith species. Then the probability that species i is absent from fractional subarea, a, is given by $(1 - a)^{N_i}$. If the species are randomly and independently distributed, then the expectation and variance of the number of species in fractional area, a are

$$E\{S\} = S - \sum_{i=1}^{S} (1 - a)^{N_i}$$

$$Var\{S\} = \sum_{i=1}^{S} (1 - a)^{N_i} - \sum_{i=1}^{S} (1 - a)^{2N_i}.$$

The availability of a theoretically based formula for the species-individuals curve should help solve the important inventory problem of estimating biodiversity through extrapolation from finite species-individual and species-area samples (e.g., Colwell and Coddington 1995).

Regional species-area relationships

The preceding considerations apply to species-area relationships on very local scales. At local scales relative abundance is more important than dispersal limitation in controlling the rate of addition of species with increased area. However, on landscape to regional spatial scales, according to the unified theory, dispersal limitation becomes far more important than relative abundance in controlling the species-area relationship. As area increases, the proportion of species that are dispersal limited increases. Also the faster the average dispersal rate, the smaller the proportion of species that will be dispersal limited for a given sized area.
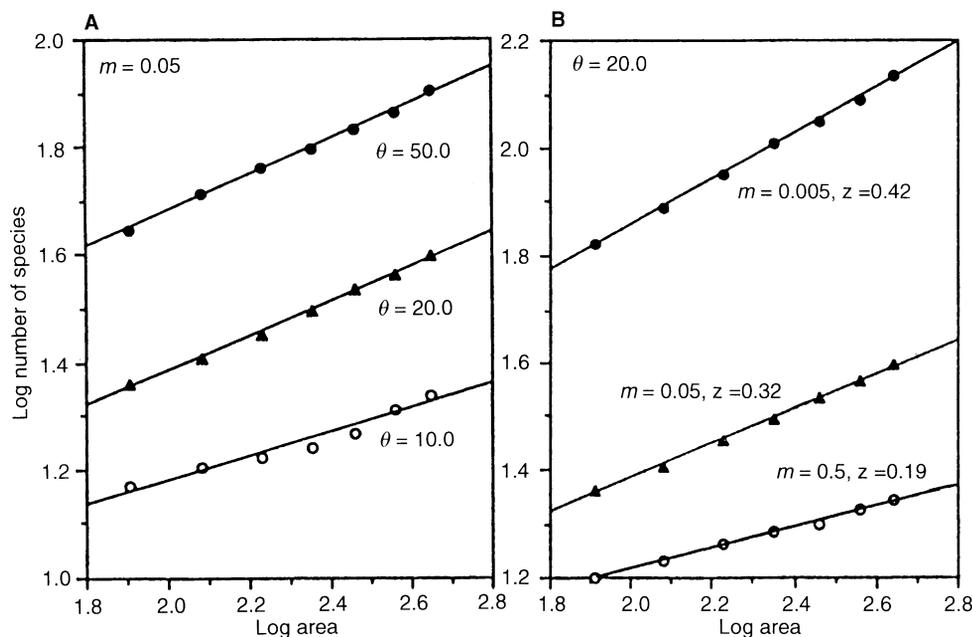
Fig. 11. A The effect of varying parameter θ on the regional species-area curve. Numerical example is a metacommunity consisting of 41×41 local communities each of size $J = 16$. The dispersal parameter m has been held constant at 0.05. The slopes of the curves are, respectively, $\theta = 10.0$, $z = 0.21$, $\theta = 20.0$, $z = 0.32$, $\theta = 50.0$, $z = 0.34$. **B** The effect of varying the dispersal parameter m on the regional species-area curve. Numerical example is a metacommunity of 41×41 local communities each of size $J = 16$. The parameter θ has been held constant at 20. Based on means of 10 simulations for 100 000 birth-death cycles

Unlike existing static sampling theories for species-area relationships, in the unified theory the species-area curve is a standing wave of biodiversity in dynamic equilibrium. This standing diversity wave is a steady-state "diversity field" defined by the combined rates of speciation, dispersal and extinction. On large, continuous landscapes, the unified theory with dispersal limitation predicts log-log linear species-area curves (Hubbell 1995, 1997; Durrett and Levin 1996), like those commonly observed in regional to continental biotas on scales larger than those on which relative species abundance dominates (Rosenzweig 1995). This effect can be seen in the straightening of the curves in Fig. 9 for large J.

The unit-area intercepts (α diversity) and slopes ("z values", β diversity) of such curves are affected both by the fundamental biodiversity number θ (Fig. 11A) and by the dispersal rate m (Fig. 11B). The parameter θ has a particularly strong effect on local α diversity and somewhat less on β diversity. The dispersal parameter m has a strong effect on both α diversity and the z slopes or β diversity. Thus, if species disperse relatively quickly across the continental landscape relative to speciation rates, then the species-area curve will have a shallow slope. Conversely if dispersal is very limited for whatever reason, then many new and local species will be encountered as sample area increases, and the species-area curve will have a steeper slope.

These results imply that there is potentially useful information about speciation rates, dispersal rates and metacommunity sizes contained in the intercepts and slopes of log-log regional species-area curves for different taxa. Although I have yet not taken the analysis very far, there are signs of interesting differences in the species-area curves for tropical trees in different plant families. In Fig. 12, I have shown the species-area curves for trees in a few plant families from data extracted from the flora of
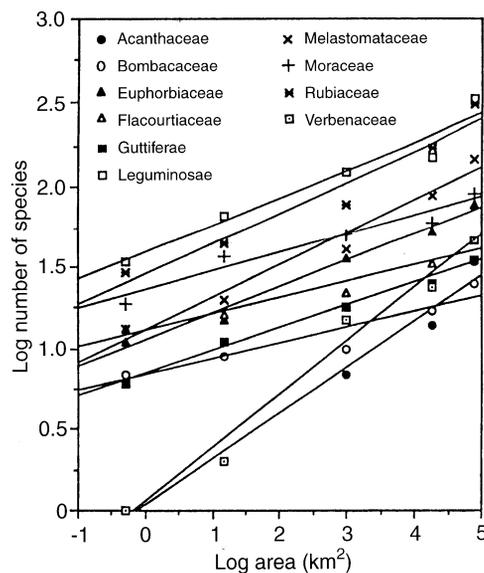
Fig. 12. Species-area curves for selected tree families in the flora of Panama. The five areas from smallest to largest are the BCI 50 ha plot; all of BCI; the former Canal Zone; the Province of Panamá; and all of the country of Panamá. Among these families, the z values range from a low of 0.097 in the Bombacaceae, a family of mainly good-dispersing heliophilic canopy emergents, to highs of 0.330 and 0.285 in the under-story shrub and treelet families, Verbenaceae and Acanthaceae, respectively

Panama (D'Arcy 1987) to illustrate the variation slope and intercept in the species-area relationships among these families. The areas vary from the 50 ha plot on BCI at the low end to all of Panama. For over 25 families with at least a dozen species in Panama, the strongest ecological correlate with the slope or z-value of the species-area

curve is adult plant height. Families of largely emergent or main canopy species tend to have higher local- or α-diversity but lower β-diversities. Conversely, families comprising mainly understory shrubs or treelets tend to have variable α-diversity, but to have large z-values and steep species-area curves, reflecting high β- diversity. This suggests that large canopy tree taxa are less dispersal-limited than small stature, understory plant taxa, and that the z values are indeed responding to differences in dispersal limitation.

The reader will no doubt realize that the diversity of species-area curves in Fig. 12 also implies that an assumption of the theory has been violated, namely that all species are identical. However, it turns out that the theory is quite robust to violation of the assumption that all species have the same per-capita dispersal and speciation rate probabilities so long as, at the landscape-level, per capita probabilities of birth and death remain the same or nearly so across all species. A more complete discussion of this issue can be found in Hubbell (1997).

Dispersal limitation and metacommunity organization

I have said almost nothing to this point about coral reefs, largely from ignorance rather than design. However, one of the defining features of most reef-building coral species is very high vagility due to the potential long-distance dispersal of their pelagic larvae. The importance of rapid dispersal is that propagules of many species reach and can potentially colonize many reefs. This in turn can dynamically couple local communities into metacommunity dynamics and regionally stabilize community composition.

The potential for dynamic coupling of local communities to the metacommunity has an important bearing on the niche-assembly versus dispersal assembly debate about the organization of ecological communities, and in particular coral reefs and rain forests. For example, recent studies of a chronosequence of uplifted fossil reef terraces in Papua New Guinea found relative constancy in taxonomic composition and in species richness extending back for 95 000 y through repeated sea-level and surface-temperature changes (Pandolfi 1996). Pandolfi (1996) concluded that this constancy was strong evidence for limited-membership coral communities, which by inference must be niche assembled. In a recent rain-forest example, Terborgh et al. (1996) reported similar dominance rankings among the 20 most abundant tree species in several 2 ha plots of terra firme forest 40 km apart along the Manu River in Amazonian Peru. Terborgh et al. (1996) also argued that this falsified the dispersal assembly hypothesis.

These conclusions are premature according to the unified theory, for several reasons. First, common metacommunity species are likely to be very resistant to extinction and to persist for geologically significant lengths of time. Second, even moderate rates of dispersal will ensure that these species are nearly everywhere nearly all the time. Third, increasing the rate of dispersal will increase the proportion of metacommunity diversity present locally.

Attempting to test the dispersal assembly hypothesis using only common species is particularly problematic.

First, there is a well known correlation between local abundance and regional abundance of species (Brown 1984, 1995), so choosing to restrict attention to common species (for whatever reason) is also to choose, in general, those species that are least likely to be dispersal limited and most likely to be persistent in space and time, biasing the conclusion toward constancy of community composition. An important result of the unified theory is that the time to complete extinction of a widespread and common species under zero-sum dynamics is extremely long (Hubbell and Foster 1986; Hubbell 1996b). The time (i.e., the number of deaths in the metacommunity) for a metapopulation of a given species to become extinct is a very large number for even moderately common species. If N_i is the metapopulation size of the ith species, then the time to extinction is $T(N_i)$:

$$T(N_i) = (J_M - 1)\left[(J_M - N_i)\sum_{k=1}^{N_i}(J_M - k)^{-1} + N_i\sum_{k=N_i+1}^{J_M-1}k^{-1}\right].$$

From θ we know that J_M is an enormous number, on the order of the inverse of the speciation rate, which is a very small number. But $T(N_i)$ is an even bigger number, on the order of the metapopulation size of the given species N_i, times the metacommunity size J_M, times the log of metacommunity size $\ln(J_M)$. The immensity of this number is important because it means that common species will be very persistent members of the metacommunity, often for geologically significant time periods. Another importance of this result is that it means that the ecological dynamics of metacommunities are temporally commensurate with the evolutionary dynamics of speciation and extinction. Indeed, this must be so because a theorem can be proven on the existence of an equilibrium diversity in the metacommunity uniquely determined by parameter θ (Hubbell 1997). This persistence means that these common metacommunity species have ample time to disperse nearly everywhere throughout the metacommunity. Evidence that widespread species are more resistant to extinction events has been provided by Jablonski (1995) and Jackson (1995).

We can illustrate the pervasiveness of common metacommunity species by plotting the incidence curves in a local community for an arbitrary species i as a function of local community size J and immigration rate m. The incidence function gives the equilibrium fraction of time or proportion of local communities in which a species is expected to be present. Consider a conservative case for a species that is only moderately abundant, comprising just 1% of the metacommunity (Fig. 13). Nevertheless, such a species will be essentially always (100%) present in local communities having more than 1000 individuals if $m > 0.1$, in communities having more than 10 000 individuals if $m > 0.01$, and in communities of more than 100 000 individuals if $m > 0.001$. For a rough sense of scale, 10 000 trees > 10 cm dbh occupy approximately 25 ha in the closed canopy forest on BCI. If we assume for sake of argument that an average coral colony occupies about 0.10 m^2, then a local reef community of 100 000 coral colonies occupies about 1 ha of reef.

It is also useful to illustrate the dynamic coupling of the local community and metacommunity by dispersal.
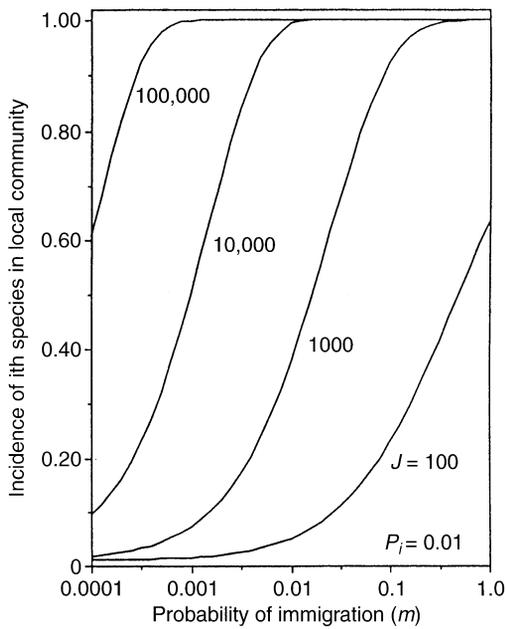
Fig. 13. Incidence curves for the local community presence of an arbitrary species i constituting 1% of the metacommunity, as a function of probability of immigration m and local community size. Local community size J was varied over 3 orders of magnitude from 100 to 100 000. Immigration rate was varied over 4 orders of magnitude, from 0.0001 to 1.0

Consider a metacommunity consisting of a landscape of 41×41 local communities each of size $J = 16$. I considered two cases of dispersal limitation, high dispersal rate ($m = 0.5$, or one immigrant for every two local deaths) and low dispersal rate ($m = 0.005$. or one immigrant for every 200 local deaths). Recall from Fig. 3 that under low

dispersal rates individual species have U-shaped probability density functions for local abundance, meaning that they are either locally extinct or locally monodominant. The metacommunity consequence of low dispersal is low local diversity and patches of monodominant species, but high regional diversity (Fig. 14). The locally monodominant communities are more resistant to local extinction by virtue of their monodominance, so more rare and local species persist in the metacommunity as a whole. Conversely under high dispersal rates, individual species are present in local communities at or near their metacommunity relative abundance. This means that local species diversity is high. However, high dispersal rates bring common species into contact with rare species, and the common species then drive rare species regionally extinct. Thus, high dispersal rates cause an equilibrium biodiversity field characterized by high local community diversity but low metacommunity diversity. Conversely, low dispersal rate causes an equilibrium biodiversity field that has low local community diversity but high metacommunity diversity.

Without data on mean dispersal rates and metacommunity species abundances, it is difficult to quantify and test these predictions for either rain forests or coral reef communities. However, one can model the dynamic coupling of local community and metacommunity in a manner that generates patterns similar to those found by Pandolfi (1996) and Terborgh et al. (1996). I computed the Bray-Curtis similarity index for communities as a function of distance in the same model metacommunities studied in Fig. 14 (Bray and Curtis 1957). This index is given by $2a/(2a + b + c)$, where a is the number of taxa common to both communities, and b and c are the taxa unique to each community. Under high dispersal ($m = 0.5$) community similarity declines only gradually with distance; whereas
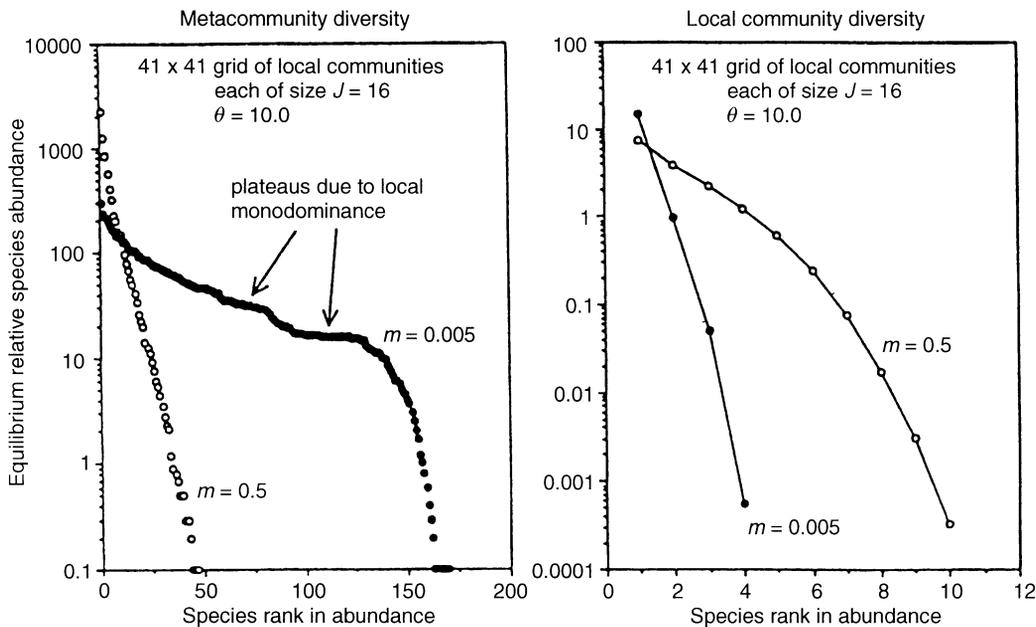
Fig. 14. Effect of high ($m = 0.5$) and low ($m = 0.005$) dispersal on the equilibrium species richness and relative abundance in local communities and in the metacommunity. Numerical example is of a metacommunity consisting of 41×41 local communities each of size $J = 16$. *Left panel*: metacommunity diversity. *Right panel*: local community diversity
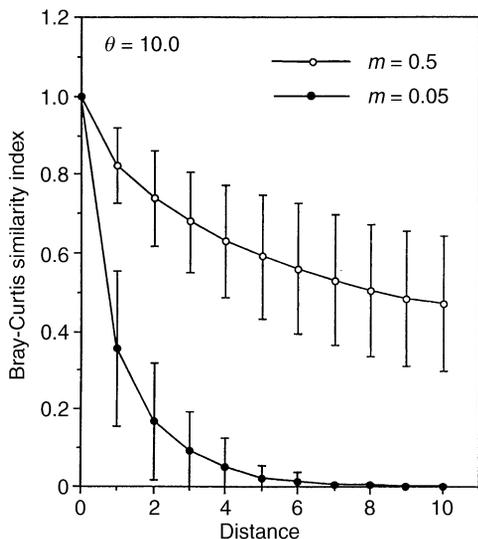
Fig. 15. Bray-Curtis index of community similarity as a function of distance separating the compared local communities in a model metacommunity consisting of 41×41 local communities each of size $J = 16$. The upper curve is the case for a high dispersal rate ($m = 0.5$), and the lower curve is for a low dispersal rate ($m = 0.005$). These couplings also change as a function of local community size J. As J gets larger, the Bray-Curtis similarity index remains higher and falls more slowly with distance

under low dispersal ($m = 0.005$) community similarity declines very rapidly (Fig. 15). In this numerical example, migration was possible in one time step only from neighboring communities. If, as in coral reefs, propagules can and often do disperse from communities very far away, then community similarities may remain very high over very long distances. Under complete mixis, the Bray-Curtis similarity index may barely drop below unity over long distances.

Conclusions

The debate over whether ecological communities are dispersal assembled or niche assembled is long standing and is probably here to stay. This is likely because both perspectives are "correct" in some sense. However, the spatiotemporal scales on which they accurately depict the structure and dynamics of natural 'communities are likely to remain fundamentally different. Recently ecologists have become increasingly interested in "macroecology" and are endeavoring to understand how many of their near and dear principles "scale up". In the end I suspect the answer will come back: "not many" in spite of some notable successes (e.g., Ricklefs and Schluter 1993; Brown 1995; Rosenzweig 1995). It is no accident, in my opinion, that the parameters of island biogeography theory are things like "immigration rate" and "island size", and not "resource supply ratio" or "prey handling time". The premise of this study is that MacArthur and Wilson (1963, 1967) were onto an important discovery, namely that a completely new set of rules and parameters govern metacommunity dynamics.

I have endeavored to show that a relatively simple generalization of the theory of island biogeography with few assumptions is capable of describing macroscopic patterns of species richness and relative species abundance in some cases with quite high precision. I believe the keys to its success are the assumption of zero-sum community dynamics and the inclusion of a speciation mechanism. The theory then shows how species richness and relative species abundance will evolve and equilibrate over a metacommunity landscape. Remarkably this happens in a perfectly homogeneous environment inhabited by perfectly identical species in terms of per capita probabilities of birth, death and migration. Of course, real species are not identical, and they have niches. But the success of the present theory suggests that most of the detail about niche structure is lost or becomes ineffective at controlling community structure on large spatial and temporal scales. Dominance arises in the model metacommunity and local community by chance and not by competitive superiority. The theory also shows how migration can stabilize local and regional community structure for long periods and over wide areas with no assumption of niche assembly or limited membership communities.

The dispersal assembly perspective is likely to be a lot more difficult to falsify qualitatively and quantitatively than might have been thought. If the predictions of the unified theory turn out to be even approximately correct for real ecological communities, then they have potentially profound implications for the contemporary theoretical paradigm in community ecology, for the organization of ecological communities, and for biogeography and conservation biology.

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