

A comment on Hubbell's zero-sum ecological drift model

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In Hubbell's model of zero-sum ecological drift, loss of species from communities by stochastic change in population size is balanced by the production of new species by processes analogous to mutation or to the fission of populations. Large regional metacommunities contain so many individuals that species are lost slowly and infrequent speciation events can maintain high diversity. However, validation of Hubbell's model requires that community size, diversity, and species life spans match up, and this is shown to be a problem with both the mutation and fission mechanisms of speciation. In the first case, most species are rare and ephemeral and would fail to be recognized by traditional taxonomic practices. In the second case, species life spans are so long that diversity builds to unrealistic levels. Thus, the problem confronting community drift probably is not the maintenance of diversity but rather its control, requiring such mechanisms as environmental change or occasional evolution of competitively superior species that sweep the metacommunity. Testing the community drift model will require close attention to community size and species life spans.

Stephen P. Hubbell, of the University of Georgia and the Smithsonian Tropical Research Institute, has produced a provocative theory linking relative abundance, diversity, and species-area relationships through a mechanism that he refers to as zero-sum ecological drift (Hubbell 2001). This mechanism takes place within a "community," which Hubbell defines as "a group of trophically similar sympatric species that actually or potentially compete in a local area for the same or similar resources" (page 5). Forest trees, which constitute the primary empirical examples in Hubbell's book, fit this definition reasonably well. In the zero-sum ecological drift model, the community has a fixed number of individuals and each individual that dies is replaced by a birth produced at random by any individual in the community. That is, births are drawn from any one species in proportion to its abundance. At the core of Hubbell's theory is the idea that community dynamics are the sum of individual dynamics, and that commu-

nity theory should arise from a consideration of the births, deaths, and movements of individuals. In particular, Hubbell argues that these properties of individuals are independent of their species identity, and this is the distinguishing feature of ecological drift. An individual of one species is the same, demographically speaking, as an individual of the next. Accordingly, with time, the number of each species fluctuates at random and species are lost from the community, just as alleles are lost from a population by genetic drift.

To maintain the diversity of a community in equilibrium, Hubbell considers two processes for creating new species: mutation and fission. In the first case, any individual birth may produce an individual of a new species, rather than of the same species, with frequency ν (the Greek lowercase letter ν). This event is equivalent to genetic mutation in an infinite-alleles model. In the second case, an individual is drawn at random from the community, and the population of the species to which it belongs is randomly divided into two portions, the smaller of which is a new species. All of Hubbell's analytical results pertain to the mutation model of species formation, although he discusses several simulations based on the fission model in Chapter 8.

To address spatial structure, Hubbell defines a metacommunity as "all trophically similar individuals and species in a regional collection of local communities" (page 5). Local communities are connected to metacommunities by a coefficient of migration (m), which represents the proportion of individuals within a local community that are replaced by offspring of individuals from outside the local community. Thus, when $m = 1$, migration does not limit membership in the local community, whose rank-abundance curve (log relative abundance versus species rank) thus parallels that of the entire metacommunity. For values of m less than one, fewer rare species can be maintained in the local

community and therefore local diversity declines and the rank–abundance curve is truncated, converting a log–series type of curve ($m = 1$) to a log–normal type of curve ($m = 0$). Species diversity within a local community is maintained against losses from extinction by local species formation or by migration of new species from elsewhere in the metacommunity.

Hubbell’s theory has already received, and will continue to stimulate, the interest and appraisal that it deserves (Zhang and Lin 1997, Yu et al. 1998, Harte et al. 1999, Abrams 2001, Bell 2001, Brown 2001, Pitman et al. 2001, Chave et al. 2002, Cody 2002, Condit et al. 2002, Enquist et al. 2002, Whitfield 2002). Tests of the theory have focused primarily on forest trees, which will be followed here. In this context, most ecologists will question the assumption of ecological equivalence among species that empirical studies have shown to be adapted for a variety of ecological roles and, to some extent at least, to be distributed nonrandomly over gradients in ecological conditions (Tuomisto and Ruokolainen 1994, Tuomisto et al. 1995, Clark et al. 1999, Vormisto et al. 2000). Random birth is also called into question by the existence of strong intraspecific density dependence in seedling establishment, which can contribute to frequency-dependent maintenance of species in a community (Schupp 1991, Wills et al. 1997, Wright 2002). Whether such exceptions to the central neutrality assumption of Hubbell’s theory will be sufficient to reject the theory outright, or will merely require quantitative adjustment of the basic predictions of theory, is as yet unclear. In this comment, I point out additional implications of the model related to the age distribution of species that will be difficult to address under any circumstances and may require a re-thinking of the basic mechanisms of species production in the model or the phrasing of predictions from the model. As will be shown, Hubbell’s model intersects fundamental questions about the nature of species and how we recognize diversity in natural communities.

Diversity and species life span

The rank–abundance curve and the diversity of a community are fully specified in the zero-sum ecological drift model by two numbers: the fundamental biodiversity number (θ , the lowercase Greek letter *theta*) and the coefficient of migration (m). Hubbell defines the fundamental biodiversity number as $\theta = 2J_M\nu$ (page 121), where J_M is the number of individuals in the metacommunity and ν is the probability of speciation per individual birth event. Hubbell states that θ is dimensionless. However, because ν represents new species per birth event [species/ind] and J_M can represent either population size [ind] or births per generation [ind/generation], $J_M\nu$ and θ have units of either [species]

or [species/generation]. Hence $J_M\nu$ and θ can alternatively represent number of species or rate of species production (Table 1).

The parameters θ and m in the zero-sum ecological drift model can be adjusted to fit practically any observed species–abundance relationship. In reference to the many empirical examples related in his book, Hubbell views this as support for the underlying model. Detractors will say that this claim merely rephrases the ease of fitting a relatively flexible mathematical function to a limited set of rank–abundance relationships (Chave et al. 2002).

The zero-sum ecological drift model makes predictions about the age distribution of species that, in principle, can also be tested against empirical data. Over the average generation time of an individual in the community, the community will experience J_M birth events and the formation of $J_M\nu = \theta/2$ new species. The average life span of a species within a metacommunity is simply the equilibrium number of species divided by the rate of production of new species (see Table 1). In the zero-sum ecological drift model, Hubbell derived the relationship between number of species (S) and number of individuals in a metapopulation (J_M) for a given fundamental biodiversity number (θ), namely,

$$S(\theta) \approx 1 + \theta \ln[1 + (J_M - 1)/\theta]$$

(page 165). When J_M is large and S is substantially greater than 1, this approaches

$$S(\theta) \approx \theta \ln(J_M/\theta),$$

which is equivalent to $S \approx -2J_M\nu \ln(2\nu)$. Accordingly, the average life span of a species in generations is approximately equal to $S/J_M\nu$, which also may be expressed as $-2 \ln(2\nu)$. Thus, average life span is inversely related to the natural logarithm of the speciation rate.

In his Figure 5.9, Hubbell fitted the zero-sum ecological drift model to the rank–abundance curve for trees having diameters at breast height exceeding 10 cm on

Table 1. The basic variables of the ecological drift model.

Variable	Explanation	Units
J_M	Individuals or births per generation	[ind] or [ind/generation]
m	Immigrant individuals per death	[ind/ind]
ν	New species per birth	[species/ind]
$J_M\nu$	Individuals \times (new species per birth)	[species]
$J_M\nu$	(Births/generation) \times (new species per birth)	[species/generation]
S	Number of species	[species]
$S/J_M\nu$	Life span = species/(species/generation)	[generations]

the 50 ha (0.5 km²) forest dynamics plot on Barro Colorado Island (BCI), Panama. The sample included 20 541 individuals of 235 species. The fitted parameters were $\theta = 50$ and $m = 0.1$. Because $m < 1$, the number of species was somewhat less than expected from a similarly sized sample taken from the entire metacommunity (estimated to be ca. 275 species). Taking the larger number for J_M , the average life span of a species would be on the order of 11 generations. Assuming 100 years per generation (Brokaw 1985, Runkle 1985, Leigh 1999), this would amount to 1100 years. (Note that some researchers have used Swaine et al.'s (1987) value of 1.7% tree mortality per year = 59 years average persistence to estimate generation time, but this does not include the time for an individual to reach a mature size. Thus, 100 years per generation is used here as an order-of-magnitude approximation.) A similar calculation for a 50-ha plot at Pasoh, Malaysia (26 331 trees > 10 cm dbh, 679 species, $\theta = 180$, $m = 0.15$), would suggest a metacommunity diversity for a comparable sample of about 800 species and an average species life span of about 9 generations. Other plant assemblages listed in Hubbell's Table 5.1 give similar average species life spans. The ratio of S/θ in several other metacommunities varied between about 3 and 10 for a variety of systems of different sizes and types of organisms (Figures 9.6–9.12).

Species life span is relatively insensitive to variation in the size of metacommunity under the mutation model of speciation. For example, for $J_M = 10^{10}$ individuals and $\nu = 10^{-8}$ ($\theta = 200$), $S = 1773$ species and the average life span is 35 generations.

At first glance, the estimated average species life spans are unrealistically short. However, according to the point mutation model of species production, new species are produced instantaneously with a population size of 1 at a rate of $J_M \nu$ per generation. This would imply 25 new species per approximately 100 years on the 50-ha plot on Barro Colorado Island and 90 on the similar-sized plot at Pasoh. Most of these new species would go extinct by "ecological drift" within one or a few generations (average time to extinction approximately $2 \ln[J_M]$) (Crow and Kimura 1970) without having attained large population sizes, and thus such species would generally be poorly sampled.

Species identities

A related problem with the estimation of θ is that species produced instantaneously would likely not have diverged sufficiently from their parent populations to be recognized as distinct species. The logical implication of this aspect of Hubbell's model is that most of the species in a community at any one time are cryptic; recognizable species make up only the tip of the diver-

sity iceberg. Yet the fitted fundamental biodiversity number is based on named species having perhaps thousands of generations of independent evolutionary history and separated from other species by chasms of genetic distance compared to the genetic variation within species. According to this logic, surveys of the plots on Barro Colorado Island and at Pasoh grossly underestimate the number of species as well as the fundamental biodiversity number even though they are complete samples for which every individual has been assigned a species name. As Hubbell points out in Chapter 8, his point mutation theory of species production results in genetic diversity within a community being concentrated close to the present. Accordingly, species boundaries should rarely be recognizable on the basis of genetic, let alone morphological, differentiation considering the large number of recently derived daughter species, regardless of their small population size (Hubbell, Figure 8.13). That "species" can be recognized at all under the point mutation model depends on few lineages having large enough population sizes to be sampled consistently and overshadow less common, cryptic sister species. Thus, what one calls species in Hubbell's model would mostly reflect deep nodes in a phylogeny, i.e. sparsely sampled monophyletic groups, within which genetic variation is not taxonomically distinguished.

In Chapter 8, Hubbell derives a function for the mean future life span or expected time to extinction (Ω , upper case Greek letter *omega*) of a species in an equilibrium metacommunity. Figure 8.7 (page 250) graphs life span versus rank for a metacommunity of $J_M = 100\,000$ and $\theta = 1, 10$, and 100. The expected number of species according to the relationship $S(\theta) \approx \theta \ln(J_M/\theta)$, gives $S(1) = 11.5$, $S(10) = 92.1$, $S(100) = 690.8$. Life spans are presented in terms of the total number of individual deaths (= births) in the metacommunity, that is, J_M deaths per generation. Using the relationship life span = $2S/\theta$, we estimate that the average time to extinction of newly formed species in these metacommunities would be 23.0, 18.4, and 13.8 generations. In terms of the total number of deaths in the metacommunity ($J_M = 10^5$), this would amount to between 2.3 and 1.4 million deaths, which is about 2–3 orders of magnitude lower than most of the data portrayed in Figure 8.7.

The discrepancy between the short average life spans of newly formed species and the long expected future life spans of extant species is due to the large population sizes of many of the species present in a community under equilibrium. Under the mutation model of species formation, many new species, whose population size initially is 1, go extinct immediately under zero-sum ecological drift. Other species present at any given time as large populations would have life spans much longer than the average. Indeed, the maximum life spans portrayed in Figure 8.7 for $\theta = 100$ are about 10^{10} accumu-

lated deaths, which for a metacommunity of $J_M = 10^5$ individuals, represents about 10^5 generations or 10 000 000 years. This is a sobering persistence time for a community under ecological drift corresponding to a tropical forested area of about 2 km², and it emphasizes that species losses under the drift model are so slow that they can be balanced by infrequent species production. For metacommunities that include billions or trillions of individuals, Hubbell (p. 251) states that maximum life spans of species would be much greater, as one might expect, however this is not quantified.

Assuming that new species are recognized only after many generations of genetic divergence, the important statistical criterion for testing Hubbell's model may be the relationship between time and population size for new species. Time to differentiate to the point of species-level recognition; time to become numerous enough to have a high probability of being sampled. Theory concerning the fixation of neutral alleles in populations (Crow and Kimura 1970) indicates that the number of generations required to reach a population size of n , regardless of the size of the community, is on the order of n . Accordingly, even species of trees with the lowest density detectable on a 50-ha plot, that is, 1 individual per 0.5 km², would have populations of 20 000 within a 100 × 100 km area, and an estimated age of at least 10 000 generations, or 1 million years. Many species would be orders of magnitude older, but these would also have younger daughter species and thus may not individually appear old in a phylogenetic reconstruction.

Although the mutation mechanism of species production permits an analytical solution to the balance between speciation and ecological drift, it is not a wholly satisfying approach. Plausible mechanisms for "mutational" speciation exist and are varied. They include karyotypic rearrangements, allo- and autopolyploidy, and invasion of a metacommunity from outside, but none of these mechanisms is likely to be important for tropical trees. Regardless, the greater difficulty for this model lies in the recognition of species as distinct entities and the sampling of rare species to obtain a useful measure of diversity.

The random fission model of species production

As an alternative, Hubbell devised the random fission model of species formation, in which a birth event is converted to a speciation event, with frequency ν , by randomly bisecting the entire population of the species to which the randomly chosen "birth" individual belongs. By its nature, the agent causing fission (that is, speciation by vicariance), whether a rising mountain chain, newly formed river course, or habitat change,

would affect many species simultaneously, thereby violating the independence assumption of community drift. This process also differs from the mutation model in that the populations of newly formed species considerably exceed 1 individual. Thus, the persistence time of new species tends to be long, and low speciation rates can result in the accumulation of many species in a metacommunity old enough to differentiate to a species-level of distinctiveness. Hubbell did not work out an analytical solution for diversity or the rank–abundance relationship for this model; such a solution may not exist. However, he presented four simulations of the process, repeated 100 times each, for a constant biodiversity number (θ) of 4 and different values of metacommunity size ($J_M = 200, 2000, 20\,000, 200\,000$). Taking data from Hubbell's Figure 8.17, the approximate relationship between S and J_M is shown here in Fig. 1.

According to the random fission model of species formation, the number of species in a metacommunity increases approximately in proportion to the square root of the metacommunity size, and indeed very close to $S = \sqrt{2J_M}$. Thus, for $\theta = 4$, we obtain the values for species diversity and life span shown in Table 2. In this example, the number of species and mean species life span increases by a factor of 10 for each 100-fold increase in J_M .

In his Figure 8.15, Hubbell plotted the rank–abundance curve for a random fission model with $\theta = 10$ and $J_M = 10\,000$, hence $\nu = 0.0005$, which yielded $S \approx 230$ species with population size > 1 . This outcome,

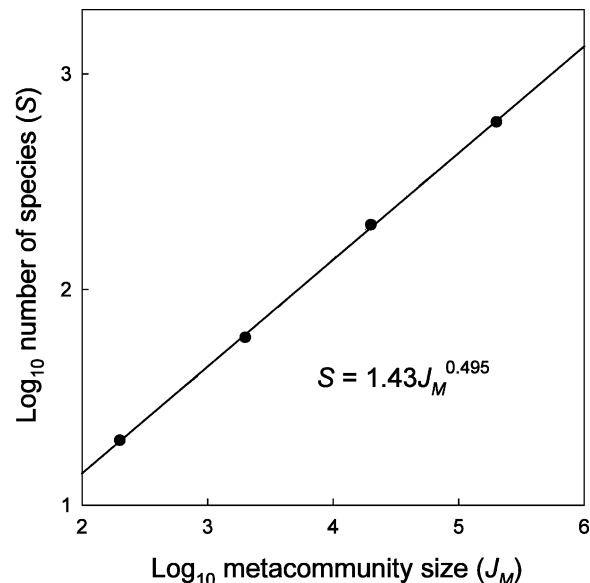


Fig. 1. Relationship between species diversity (S) and metacommunity size (J_M) in four simulations with $\theta = 4$ and $J_M = 200, 2000, 20\,000, \text{ and } 200\,000$ (from Hubbell 2001, Fig. 8.17).

Table 2. Relationship between diversity (S), metapopulation size (J_M), and species life span for $\theta = 4$ (from Hubbell 2001, Fig. 8.17, the last five entries by extrapolation).

J_M	S	v	Mean life span = $2S/\theta$
200	20	10^{-2}	10 generations
2000	60	10^{-3}	30
20 000	200	10^{-4}	100
200 000	600	10^{-5}	300
2×10^6	2000	10^{-6}	1000
2×10^7	6000	10^{-7}	3000
2×10^8	20 000	10^{-8}	10 000
2×10^9	60 000	10^{-9}	30 000
2×10^{10}	200 000	10^{-10}	100 000

Table 3. Comparison of diversity and species life span under the mutation and fission models of species production.

	Mutation model	Fission model
Number of species	$-2J_M v \ln(2v)$	$J_M v^{1/2}$
New species per generation	$J_M v$	$J_M v$
Average species life span	$-2 \ln(2v)$	$v^{-1/2}$

combined with the data set out in Table 2, is consistent with the following approximation for the number of species, $S \approx \sqrt{\theta J_M / 2} = J_M \sqrt{v}$. Accordingly, the average life span of a species from the point of its formation is $1/\sqrt{v}$, which is independent of the metacommunity size. Thus, for a given speciation rate, the number of species increases in direct proportion to the size of a metacommunity. For low speciation rates, the average life span of a newly formed species is much longer than in the mutation model of species production because of the larger initial population size, as set out in Table 3.

Tropical forest trees number about 40 000–80 000 per km^2 , based on counts on the 50-ha plots on BCI and at Pasoh (Hubbell 2001) and plots in upper Amazonia (Pitman et al. 2001). It is difficult to estimate the size of a metacommunity. However, considering the broad distributions of some species of trees in the Neotropics (Condit et al. 2002), a dimension of 500 km, yielding a

metapopulation area of 250 000 km^2 , is reasonable for purposes of illustration (Pitman et al. 2001). Thus, one might consider a metacommunity size of $J_M = 40\,000 \times 250\,000 = 10^{10}$ individuals. Let us suppose that the average life span of species in natural communities is no more than 10^7 years, or 10^5 generations, for which the corresponding fission rate is 10^{-10} . Accordingly, the equilibrium number of species in such a metacommunity would exceed $J_M \sqrt{v} = 10^{10} \times 10^{-5} = 10^5$, or about 100 000 species. A more reasonable number of species, on the order of 10^4 , in such a metacommunity, would imply an average species life span of 10^6 generations (10^8 years) or a metacommunity size under 10^9 individuals, that is, a square area of 2.5×10^4 having a linear dimension of about 160 km!

The dilemma of the fission model of species production differs from that of the mutation model. The mutation model produces large numbers of ephemeral “species” that are difficult to recognize and to sample. The fission model results in larger populations with moderate life spans on the order of 100’s to 100 000’s of generations, but it predicts too many species in equilibrium metapopulations of reasonable size and with species life spans of reasonable length. In the ecological drift model, species persist much too long. This is good news in that infrequent speciation events can maintain diversity without having to resort to other stabilizing mechanisms, but it’s bad news in that too many species accumulate. Molecular phylogenetic analyses eventually will provide distributions of the ages of species in metacommunities, however an average of 10^6 years, or 10^4 generations, would probably not be off by much.

The relationship between number of species, community size, and rate of species production in the fission model are set out in Table 4. Under Hubbell’s fission model of speciation, reasonable numbers of species for tropical forests (10^3 – 10^4) are consistent with either unrealistically small metacommunities or unrealistically low speciation rates with correspondingly long species life spans. For less diverse temperate forests (S approx. 10^2 – 10^3 species, Latham and Ricklefs 1993), the numbers are even less probable.

Table 4. Correspondence between species diversity (S), metacommunity size (J_M), and speciation rate (v) according to the fission model of species production.

Speciation rate	Metacommunity size (J_M , ind)					Ave. life span	
	10^{10}	10^9	10^8	10^7	10^6	Gens.	Years
10^{-4}	$S = 10^8$	10^7	10^6	10^5	10^4	10^2	10^4
10^{-6}	10^7	10^6	10^5	10^4	10^3	10^3	10^5
10^{-8}	10^6	10^5	10^4	10^3	10^2	10^4	10^6
10^{-10}	10^5	10^4	10^3	10^2	10^1	10^5	10^7
10^{-12}	10^4	10^3	10^2	10	1	10^6	10^8
Area (km^2) =	2.5×10^5	2.5×10^4	2.5×10^3	2.5×10^2	2.5×10		

Numbers in boldface type bracket the range of observed numbers of tree species.

The challenge of community drift

Hubbell's model of zero-sum ecological drift provides an alternative against which to compare other models of the regulation of community diversity that incorporate within- and between-species interactions (Chave et al. 2002). It also raises questions about how we incorporate regional processes, such as species production by the fission model, into the dynamics of local communities. Hubbell has developed one approach to this problem with individual-based models that incorporate spatial structure. The most problematic aspect of Hubbell's model is to relate his mechanisms of species production to species concepts used in taxonomy. How are we to recognize and sample species produced by the mutation model? Does fission occur within a metacommunity, or does allopatry, which is a reasonable analog of fission, suggest that "fission" results from the splitting of metacommunities or invasion from outside a metacommunity? Molecular phylogenetic analyses may begin to address these questions as long as sampling of terminal "taxa" is not constrained by conventional species limits and as long as markers are sensitive enough to record recent separation of lineages. Should such studies apply a phylogenetic or a biological species definition?

The size of the metacommunity for temperate and tropical forests must be on the order of at least 10^{10} individuals, and perhaps many more in core areas of diversification, such as the Amazon Basin, Malesia, and temperate eastern Asia. Provided this estimate is reasonable, do the estimates of diversity and species life spans add up? The mutation model of species production predicts many "species" of short duration. For example, for a metacommunity of 10^{10} individuals and 10^3 species, the mutation rate would be approximately 3×10^{-7} and the average life span of a newly formed species would be 29 generations. In contrast, the fission model produces new species with large populations and long life spans, resulting either in too many species or species durations that are unrealistically long. For the same metacommunity of 10^{10} individuals and 10^3 species, the fission model requires a speciation rate of 10^{-14} , which corresponds to an average species life span of 10^7 generations.

To make any sense at all, the mutation model requires a lower rate of species production and mechanisms to increase the persistence of newly formed species. Frequency dependent effects on survival and birth, which tend to counter loss by drift when population size is small, can enhance persistence. The theory of the balance between selection and drift in population genetics indicates that the probability of fixation of a mutant is approximately twice its selective value (s) when s is small and approximately the selective value when s is large (Crow and Kimura 1970). By analogy, for example, when an individual representing a newly

formed species has a 5% greater than neutral chance of survival, it has a 10% chance of becoming fixed in the community. With a 50% greater than neutral chance of survival, the probability of fixation is close to 60%. Thus, relatively strong competitive advantage to rare species would increase persistence and permit a given level of diversity to be maintained with a lower rate of species production (Yu et al. 1998).

The fission model, by which new species originate as substantial populations, seems more realistic than the mutation model, but has the opposite problem in that species persist too long. In large metacommunities, drift is a weak force of extinction. To make any sense, the fission model of speciation requires mechanisms to shorten the life spans of species and cause higher extinction rates. In terms of the structure of Hubbell-like models, this would require the appearance of competitively superior species that occasionally swept communities and caused the extinction of other species, thereby ensuring a higher rate of turnover for a given number of species. Of course, a realistic model would require that all of these processes be diversity dependent (Rosenzweig 1975, 1995).

Testing the community drift model

A pressing concern for community ecology should be to test Hubbell's model. An adequate test of the model must include an evaluation of its basic assumptions as well as its ability to fit data compared to that of models incorporating competition and niche partitioning. This will not be an easy task. The first problem in any study of diversity is the definition of species. If the mutation model of species production were to pertain, most species would be young and rare, often missed because of failure to recognize them as separate species or failure to sample them. In this case, there remains a problem of reconciling empirical observation with theory, and it is unlikely that Hubbell's ideas can be tested meaningfully, at least at the present time. If we assumed that the fission model is more likely, a given speciation rate would result in fewer species with higher average abundance and longer average life span. Thus, species would be easier to identify and sample.

Supposing that we can recognize species, determine their relative abundance, and perhaps determine the distribution of their ages, several tests of Hubbell's theory become possible. Because ecological drift is a stochastic process, samples of local communities removed in space or time should have low correlations between their species composition. For example, Pitman et al. (2001) argued that because local communities 1400 km distant in Ecuador and Peru had a high correlation among their more common species, community composition was stabilized by non-stochastic pro-

cesses. In principle, the same argument would apply to communities in the same place separated by time, for example a fossil assemblage and a contemporary community. The relation between process and community correlation has meaning, however, only when the temporal and spatial dynamics of the ecological drift model can be used as a meter stick for comparison. Remembering that under community drift, the average life expectancy of the more common species in a meta-community can be thousands of generations, distances on the order of 1000 km may not be sufficient to break down community correlations, particularly among the more abundant species. The theory of population genetics tells us that the movement of only a single individual per generation between two sub-populations is enough to counter the diverging tendency of genetic drift. Thus, correlation over distance must be judged on a scale of dispersal distance. Pitman et al. (2001) point out that community correlations decrease rapidly with distance in Panama (Pyke et al. 2001) but central Panama is heterogeneous ecologically, having a steep rainfall gradient over a distance of tens of kilometers. Hence, it might not be a useful gauge for distance–correlation relationships among similar habitats in Amazonia (Condit et al. 2002).

It is unlikely that correlations over time will be much more useful for testing community drift. The time scale of change through community drift, which in generations is on the order of the community size in individuals, is almost certainly longer than the time scale for environmental change in a given place. During the recent period of earth history, major environmental change has taken place on the scale of 10^3 to 10^6 years, or 10 to 10 000 generations of trees – much too rapid for drift to produce changes in abundance–rank relationships that can be distinguished from environmental effects.

A possibility for testing drift theory lies in the relaxation of diversity following the isolation of islands or habitat patches (Diamond 1972, Terborgh 1974, Wilcox 1978, Case and Cody 1987). Many islands on continental shelves became cut off from the nearby mainland by rising sea levels following the melting of the glaciers 18 000–10 000 years ago. Most of these islands currently support fewer species than comparable areas of the mainland, which has been attributed to the lack of immigration of individuals from surrounding areas, the so-called rescue effect (Brown and Kodric-Brown 1977) or mass effect (Shmida and Wilson 1985). In these settings, we may ask whether the rate of species loss is compatible with ecological drift or reflects additional processes (Leigh et al. 1993). If we ignore new species and assume stochastic fluctuation in population size with equal birth and death rates (not exactly zero-sum ecological drift, but close), we would expect 50% of populations of initial

size i to have disappeared by $t_{50} = 0.5^{1/i}/(1 - 0.5^{1/i})$, or approximately $i\sqrt{2}$ generations (Pielou 1977). Thus, over a period of 10 000 years (about 100 generations), one might expect the extinction of half of the populations having initial sizes of 70 individuals. This approach might yield some very specific predictions about species loss on land bridge islands under ecological drift and constant conditions. Leigh et al. (1993) determined that species diversity in isolated communities under ecological drift should decline at an exponential rate of $-2/N$, where N is the number of individuals of all species in the community. However, species of trees disappeared more rapidly than predicted by drift from <1 ha islands isolated for ca 80 years by the formation of Gatun Lake, Panama, and Leigh et al. suggested that increased wind exposure and absence of mammalian seed predators accounted for the rapid changes.

To my mind, the most prominent feature of Hubbell's community drift model is the length of time that established species under the mutation model, or even newly formed species under the fission model, persist in communities of any size. Before deciding on the merits of the model for a particular community or metacommunity, it will be necessary to define and tabulate species in a manner consistent with the model of species formation, to measure the size of the metacommunity or local community, quantify the rate of migration between the local community and the metacommunity, and determine that significant community change can occur on a shorter scale than environmental change. I suspect that the stumbling block for Hubbell's model is that communities don't change fast enough under community drift. Changing environments, invasion of metacommunities from outside, evolution of competitive relationships, especially when competitive ability is influenced by host–pathogen interactions – all these processes are likely to occur more rapidly than species are lost from communities by drift and they will therefore shape community composition more powerfully than stochastic processes. The problem may not be to stabilize a randomly drifting community composition by resource partitioning and frequency-dependent equilibrium coexistence, but rather to accelerate change and prevent the excessive accumulation of species, perhaps through environmental change or the occasional evolutionary acquisition of competitive dominance. Regardless of the eventual outcome of tests of community drift, Hubbell's theory forces us to take a much closer, quantitative look at communities over varied scales of time and space than we have been accustomed to in the past.

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