

THE UNIFIED NEUTRAL THEORY OF BIODIVERSITY: DO THE NUMBERS ADD UP?

ROBERT E. RICKLEFS¹

Department of Biology, University of Missouri–St. Louis, 8001 Natural Bridge Road, St. Louis, Missouri 63121-4499 USA

Abstract. Hubbell's unified neutral theory is a zero-sum ecological drift model in which population sizes change at random in a process resembling genetic drift, eventually leading to extinction. Diversity is maintained within the community by speciation. Hubbell's model makes predictions about the distribution of species abundances within communities and the turnover of species from place to place (beta diversity). However, ecological drift cannot be tested adequately against these predictions without independent estimates of speciation rates, population sizes, and dispersal distances. A more practical prediction from ecological drift is that time to extinction of a population of size N is approximately $2N$ generations. I test this prediction here using data for passerine birds (Passeriformes). Waiting times to speciation and extinction were estimated from genetic divergence between sister populations and a lineage-through-time plot for endemic South American suboscine passerines. Population sizes were estimated from local counts of birds in two large forest plots extrapolated to the area of wet tropical forest in South America and from atlas data on European passerines. Waiting times to extinction (ca. 2 Ma) are much less than twice the product of average population size (4.0 and 14.4×10^6 individuals in South America and Europe) and generation length (five and three years) for songbirds, that is, 40 and 86 Ma, respectively. Thus, drift is too slow to account for turnover in regional avifaunas. Presumably, other processes, involving external drivers, such as climate and physiographic change, and internal drivers, such as evolutionary change in antagonistic interactions, predominate. Hubbell's model is historical and geographic, and his perspective importantly links local and regional process and pattern. Ecological reality can be added to the mix while retaining Hubbell's concept of continuity of communities in space and time.

Key words: community diversity; ecological drift; extinction; neutral theory; passerine birds; population size; regional diversity; speciation.

INTRODUCTION

Hubbell (1979, 2001) proposed an individual-based, stochastic theory to explain patterns of species richness in ecological communities. He called this the unified neutral theory of biodiversity. As in other neutral theories (see Chave [2004] for a review), Hubbell's model is one of zero-sum ecological drift, meaning that a community has a fixed number of individuals and that each random death is replaced by the single offspring of a random individual regardless of the identity or size of its population. Consequently, there is no frequency or density dependence. Many authors have commented upon Hubbell's model, both positively and negatively. Rather than reviewing these arguments, I shall focus on testing some quantitative predictions of the model using data on passerine birds, for which critical parameters of ecological drift can be estimated.

Hubbell's model is identical to random genetic drift of neutral alleles in a single-locus, infinite-alleles model for

a haploid population with overlapping generations. Under both genetic and ecological drift, the entire population eventually is composed of the descendants of a single allele (or individual) present in the population at some time in the past, referred to as the coalescence time (Hudson 1990). Thus, one allele (or one type of individual, i.e., species) becomes fixed while all others become extinct and diversity drops to zero. In both genetic (Kimura and Ohta 1971, Kimura 1983) and ecological drift models, the tendency towards extinction can be balanced by the creation of new diversity through mutation or species formation. Indeed, to find an analytical solution to the equilibrium diversity in a community, Hubbell (2001:114) modeled speciation as a mutation event. Accordingly, a random offspring of a single individual would become transformed into a new species, which initially would have a population size of a single individual.

Zero-sum ecological drift is purely geographical and historical. The equilibrium number of species in the regional "community" (or metacommunity) depends only on the total number of individuals (J_M , a function of geographic extent and population density) and the rate of speciation (ν , the lowercase Greek nu). Local communities including J individuals are part of the larger metacommunity and connected to it by migration,

Manuscript received 20 May 2004; revised 2 December 2004; accepted 7 December 2004. Corresponding Editor: M. Holyoak. For reprints of this Special Feature, see footnote 1, p. 1368.

¹ E-mail: ricklefs@umsl.edu

at rate m . The relative importance of migration compared to species formation in maintaining diversity increases with decreasing size of the local community. Migration slows change in local communities over time. This effect can be extended to the turnover of species (beta diversity) in a continuous landscape by introducing limited dispersal distance for the offspring of each individual (Chave and Leigh 2002, Condit et al. 2002).

Hubbell's theory is unifying because it brings together, in a single model, predictions concerning the number and relative abundance of species within communities, the relationship of diversity to area, and the turnover of species with distance. This is a remarkable accomplishment. However, the relevance of Hubbell's model to ecologists depends on the degree to which it describes the real world. Many believe that it does not, because their experience with nature suggests that density dependence (Wills et al. 1997) and habitat specialization (Tuomisto and Ruokolainen 1994, Tuomisto et al. 1995, Clark et al. 1999, Duivenvoorden et al. 2002, Potts et al. 2002), both of which violate the premises of Hubbell's model, are fundamental features of ecological systems.

Hubbell's theory makes several quantitative predictions that can be tested against observations. Two of these predictions have received considerable attention. One is the particular form of the relative abundance curve within communities (McGill 2003, Volkov et al. 2003, Etienne and Olf 2004, Potts et al. 2004). When migration is infinite and the local and regional communities coincide, the form of the rank-abundance relationship assumes a log-series distribution, which can be described by a single parameter, Fisher's alpha (α ; Fisher et al. 1943, Magurran 1988) for a given community size (number of individuals, N , which is the same as Hubbell's J). Alpha is linked to Hubbell's model in the following way. When new species are formed by individual mutation, species richness is determined by a single "fundamental biodiversity number," theta (θ), which is related to community size and speciation rate as $\theta = 2Jv$. For a given biodiversity number, species richness is approximately $S(\theta) \approx \theta \ln(J/\theta)$. In the absence of migration, θ is asymptotically equivalent to Fisher's alpha. Migration to local communities at rate m distorts the log-series form of the rank-abundance curve in a predictable manner, and most rank-abundance curves can be fitted by some combination of values of J , v , and m (e.g., Hubbell 2001:131). It should be evident, however, that without measuring J , v , and m independently, this "test" becomes an exercise in curve fitting rather than hypothesis testing.

A second prediction that has been used to test Hubbell's theory addresses the turnover of species with respect to distance (Durrett and Levin 1996, Pitman et al. 2001, Chave and Leigh 2002, Condit et al. 2002). The theory predicts that the correlation in abundance between species should decrease with distance when dispersal is limited, but the rate of decrease depends on the speciation rate and the dispersal distance. Without

knowing these parameters, which are not part of the drift mechanism itself and thus are external variables, such tests of Hubbell's model involve too many unknowns and are ambiguous.

Other predictions of Hubbell's model concern changes over time. Because the abundances of species within communities are stochastic variables, the variance in the abundance of each species among local communities increases linearly with time. Clark and McLachlan (2003) tried to test this prediction using the abundance of tree species in fossil pollen from cores of Holocene lake sediments in eastern North America. They found, contrary to Hubbell's model, that variance in abundance among sites did not increase, but remained relatively stable over a period of 5000–7000 yr, or about 50–70 generations. This is a relatively weak test, however, because the time since the revegetation of glaciated North America was not sufficient for the establishment of equilibrium under ecological drift, and 50–70 generations would probably produce little change in the frequencies of abundant trees in a community of millions of individuals. Furthermore, dispersal across the region from which the samples were taken (about three degrees of latitude, or 330 km, and four degrees of longitude at 45 N, or about 316 km) might be sufficient to prevent community divergence under any circumstance. Without knowing population size and dispersal distance, such a test of Hubbell's model is inconclusive.

DRIFT AND TIME

At this point, the most unambiguous test of Hubbell's model addresses time itself. Drift takes time; the larger the community, the longer it takes (Hubbell 2001:83). For example, when birth and death are stochastic processes having equal rates, the probability of extinction increases with time and reaches $1/e$ (0.37) in approximately N generations, where N is the initial size of the population (Pielou 1969:17 ff). Leigh (1981) determined that the average time to extinction under neutrality when a population cannot exceed size K is equal to $2N(1 + \ln[K/N])$, which is at least $2N$. Leigh (1981:219) pointed out that this result for extinction "agrees with Fisher's (1930) calculation that the number of descendants of a single neutral mutant will not exceed a small multiple of the number of generations elapsed since the mutant occurred." That is, under neutrality the increase and decrease in the number of alleles or individuals in a population are mirror images in time (see also Kimura and Ohta 1971). Thus, the expected time to extinction of a population of size N is minimally $2N$ generations, as is the period required for a single mutant (or newly formed species of size 1) to increase by drift to N individuals. Furthermore, the time required for the number of species and their relative abundances to approach equilibrium under genetic drift is several multiples in generations of the total size of the community in individuals (K or J). Leigh (1981) pointed out that for some kinds of communities the expected life

spans of the commonest species, not to mention the time to equilibrium of the entire community, would exceed the age of the earth.

Under a mutation model of speciation, species richness in a metacommunity (S) with neutral dynamics is related to metacommunity size (J_M) and rate of speciation (v) according to $S \approx -2vJ_M \ln(2v)$ (Hubbell 2001:165, Ricklefs 2003). This provides a testable relationship, but while the mutation model allows an analytical solution to the equilibrium number of species, it does not portray species formation realistically. Alternatively, Hubbell (2001:264) devised a fission model whereby a population of one species would split at random into two species. Each daughter species would contain a random fraction of the individuals in the parent species.

Hubbell was not able to derive an analytical solution for the equilibrium number of species under a fission model of speciation, but we may use the following logic to find an approximate solution. According to the fission model, a random individual from a metacommunity of size J_M is chosen with probability v and the species to which it belongs (population size N) is then cleaved randomly into two parts. The probability that a particular population will undergo fission is vN and the rate at which new species form by this process in the metacommunity as a whole is vJ_M . The time in generations to extinction in a drift model is approximately twice the population size (Leigh 1981), which, on average, is twice the total size of the metacommunity divided by the number of species ($2J_M/S$). Thus, the average rate of extinction per species is the inverse, $S/2J_M$, which, multiplied by the number of species, provides the overall rate of extinction in the community, $S^2/2J_M$. At equilibrium, extinction equals speciation, that is, $S^2/2J_M = vJ_M$, and $S = J_M\sqrt{2v}$.

Regardless of whether extinction occurs at a rate consistent with drift, or at some other rate, for example resulting from species interactions in a heterogeneous environment, speciation and extinction will come into balance. Accordingly, knowing S and J_M , one could estimate the speciation rate v . However, neutral theory makes no prediction about the time to speciation; rather, extinction provides the critical test of neutrality. If one assumes that extinction and speciation rates are approximately balanced, then the time to extinction will equal the time to speciation, $2J_M/S$. Thus, knowing J_M and S , one can ask whether Hubbell's model predicts a plausible average time to extinction. In other words, do the numbers add up? In an earlier comment on Hubbell's theory (Ricklefs 2003), I expressed some doubt about this with respect to tree species richness in Neotropical forests. Considering the large metacommunity sizes (on the order of 1×10^{10} individuals), large number of species (perhaps 2×10^4), and long generation times of trees ($\sim 1 \times 10^2$ yr), it seemed that drift runs too slowly (perhaps 1×10^8 yr to extinction), a point made earlier by Leigh (1981).

In this article, I use estimates of population sizes and rates of speciation in songbirds (Passeriformes) to test the prediction that time to extinction is about twice the average population size of a species. Songbirds differ from forest trees as a model system for this purpose because they have relatively short generation times and are several orders of magnitude less abundant. I based the following analyses on data for passerine birds from South America, North America, and Europe.

ESTIMATION OF SPECIATION AND EXTINCTION INTERVALS

Use of molecular phylogenies

In a random speciation process, the time between speciation events is exponentially distributed with mean $1/\lambda$, where λ is the rate of speciation. In a phylogenetic tree, the most straightforward estimate of $1/\lambda$ is the average length of internal branches. In practice, this is unrealistic to the extent that taxon sampling is incomplete and extinction has erased the evidence of internal nodes. Terminal branches suffer less than internal branches from the problem of extinction and their average length estimates approximately one-half the distance between speciation events. Where taxon sampling is complete, genetic distance between sister taxa, which is commonly reported in the literature, can be used to estimate genetic distance between speciation events along a branch. Genetic distance can be converted to time by a suitable calibration. For mitochondrial DNA (mtDNA) sequences, a commonly used calibration is 2% sequence divergence between sister taxa per million years (Shields and Wilson 1987, Klicka and Zink 1997, Fleischer et al. 1998, Lovette 2004).

Estimates of the average mtDNA sequence divergence between presumed sister species vary between about 1.9% and 5.1%, with a range for individual pairs between 0% and almost 11% (Klicka and Zink 1997, Avise and Walker 1998, Johns and Avise 1998, Johnson and Cicero 2004, Lovette 2004). Assuming an overall average of 4%, the average time between speciation events for passerine birds would be about 2 million years (Ma).

Use of lineage-through-time plots

Harvey et al. (1994) showed how one can use a lineage-through-time (LTT) plot to estimate speciation and extinction rates within a clade. The LTT plot portrays through time the number of lineages ancestral to present-day extant species (Fig. 1). When speciation rate (λ) and extinction rate (μ) are constant through time (t), the logarithm of the number of lineages increases linearly with time at rate $\lambda - \mu$. However, because phylogenetic reconstructions, from which LTT plots are constructed, do not include extinct lineages, lineage accumulation is not strictly linear. The number of lineages ancestral to extant species (the realized line) increases more rapidly towards the present because progressively fewer recently produced lineages have had time to go extinct (Fig. 1). Thus, the slope of the lineage

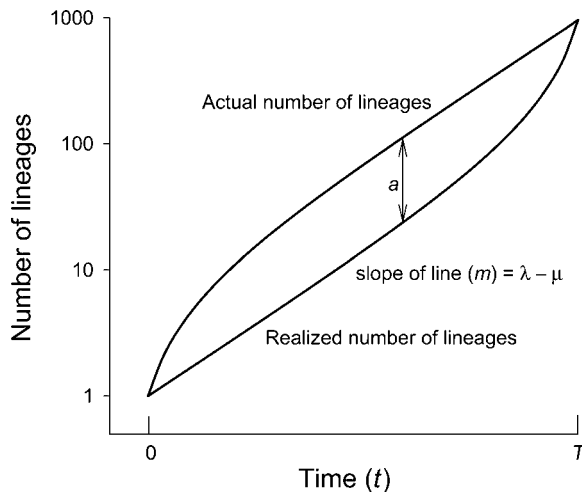


FIG. 1. Theoretical shapes of actual and realized lineage-through-time plots (after Harvey et al. [1994]), showing the slope (m) and separation of the two plots (a) used to estimate speciation (λ) and extinction rates (μ) from the relationships $m = \lambda - \mu$ and $a = -\ln(1 - \mu/\lambda)$. Note the log scale of the y-axis.

accumulation curve approaches the speciation rate λ as the curve approaches the present.

On an LTT plot, the slope of the near-linear portion of the realized line represents approximately the net diversification rate, that is, $\lambda - \mu$. The difference between the actual and the realized lines (a) is equal to $-\ln(1 - \mu/\lambda)$, which can be rearranged to give $\lambda = (\lambda - \mu)/\exp(-a)$. Thus, knowing $\lambda - \mu$ and a , one can estimate λ and, by subtraction, μ . Although one cannot measure the actual number of lineages at any given time in the past, the actual and realized lines are parallel in the middle of the time span, both having slopes approaching $\lambda - \mu$. A reasonable approximation to the actual number of lineages through time is a line with slope $\lambda - \mu$ that passes through the contemporary number of species. Thus, one can estimate a by extrapolating the linear part of the realized LTT plot to the present (time T) and subtracting the extrapolated number of species from the actual number of species.

I extracted a lineage-through-time plot for all of the South American members of the Parvorder Tyrannida from the DNA-DNA hybridization-based phylogeny of Sibley and Ahlquist (1990). The relative times of lineage splitting are indicated by the difference in melting point temperatures (ΔT_{H50} , °C) between heteroduplexed and homoduplexed hybridized DNA. The Tyrannida represent a large radiation of suboscine passerine birds endemic to South America and subsequently to tropical parts of Central America, with a small number of lineages extending to temperate regions of North America. The clade is represented by 966 species in South America (Meyer de Schauensee 1966). Sibley and Ahlquist (1990) obtained DNA samples from 111 species representing most of the genera and virtually all of the higher clades. The lineage-through-time plot is

linear through much of the history of the group, suggesting a relatively time-homogeneous rate of diversification (Fig. 2).

Because Sibley and Ahlquist did not sample all species of the clade, the slope of the lineage-through-time plot falls off towards the Recent. However, one can anchor the plot in the present (time T) by the contemporary number of species in the group. I estimated the slope of the LTT plot by linear regression using 36 points from the base of the clade up to a depth of $\Delta T_{H50} = 5^\circ\text{C}$. Most genera branch from nodes more recent than this point, and so Sibley and Ahlquist's representation of lineages up to this depth in the phylogeny is probably relatively complete. The slope of this line, which estimates the net rate of diversification is $\lambda - \mu = 0.313 \pm 0.005 \text{ }^\circ\text{C}^{-1}$. Extrapolating this line to the present ($\Delta T_{H50} = T$), gives a value of 5.176 ± 0.045 (natural log of 177.0 species), and the estimated difference between the actual and realized lines is 6.873 (natural log of 966 species) $- 5.176 = 1.697$. From this, we can estimate $\lambda = 1.71$ and $\mu = 1.71 - 0.31 = 1.40 \text{ }^\circ\text{C}^{-1}$. Thus, the extinction rate in this growing clade has been about 82% of the speciation rate.

Absolute rates of speciation and extinction require calibrating Sibley and Ahlquist's ΔT_{H50} scale against

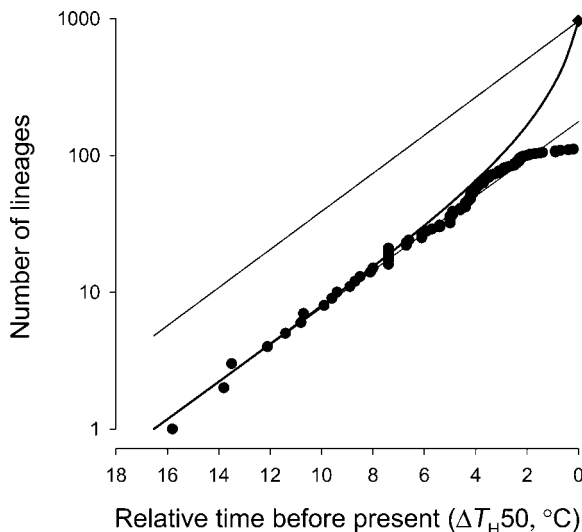


FIG. 2. Realized lineage-through-time (LTT) plot based on a DNA-hybridization phylogeny of 111 species of the South American Tyrannida clade (Sibley and Ahlquist 1990) and the 966 species of Tyrannida in the contemporary South American avifauna. Relative times of lineage splitting are indicated by the difference in melting point temperatures (ΔT_{H50}) between heteroduplexed and homoduplexed hybridized DNA. The slope of the lower straight line ($\lambda - \mu$) is estimated from the 36 branch points up to a relative time of $\Delta T_{H50} = 5^\circ\text{C}$. The value of a (difference between the actual and realized lines) was estimated from difference between the extrapolated value of the fitted line at time 0 and the total contemporary number of species. The parallel upper straight line represents the more recent part of the actual LTT plot with slope $\lambda - \mu$ and an intercept equal to the contemporary diversity. The heavy curved line is the realized LTT curve calculated according to Harvey et al. (1994).

time, assuming a linear relationship. In the Sibley-Ahlquist phylogeny, the oscine-suboscine split within Passeriformes has a molecular divergence of $\Delta T_{H50} = 19.7^\circ\text{C}$. The oldest fossils of passeriform birds date to about 55 Ma (Boles 1997), but these bone fragments cannot be assigned to any subgroup within the Passeriformes. Calibrated molecular clock estimates have placed the oscine-suboscine split at 77 Ma (van Tuinen and Hedges 2001) and 66–70 Ma (Harrison et al. 2004). This might be too old, considering the absence of fossils attributable to either oscines or suboscines prior to the Miocene (e.g., Mayr and Manegold 2004). Thus, $1^\circ\text{C} \Delta T_{H50}$ equals, at most, approximately 4 Ma, based on van Tuinen and Hedges's estimate, but probably no less than 2 Ma.

Using the longer calibration time, we may estimate the speciation rate for South American suboscines to be 1.71 per 4 Ma, or approximately 0.43 per Ma, which corresponds to an average waiting time between speciation events of $1/0.43 = 2.34$ Ma. Alternatively, using the shorter calibration time, the waiting time would be 1.17 Ma. These values are similar to estimates of speciation intervals based on mtDNA divergence and assuming 2% sequence divergence per Ma (4% = 2 Ma). If we assume that $\mu = 0.82\lambda$, the average waiting time between extinction events would be either 2.86 or 1.43 Ma.

The average annual mortality (M) rate of Neotropical passerine birds is probably close to 0.25 yr^{-1} (Karr et al. 1990, Brawn et al. 1995, 1999, Johnston et al. 1997, Ricklefs 1997) which, allowing one year to maturity, corresponds to a generation time of approximately $1 + 1/M = 5$ years. Thus, the waiting time to extinction, which is the average time to extinction of a newly formed species, would be approximately $2.86/5 = 0.57$ or $1.43/5 = 0.29$ million generations.

ESTIMATION OF POPULATION SIZE AND TIME TO EXTINCTION

Tropical forest birds

Detailed censuses are available for two Neotropical forests: a 97-ha plot of floodplain forest in Amazonian Peru (Terborgh et al. 1990) and a 100-ha plot in primary rainforest of French Guiana (Thiollay 1994). For each of these plots, I considered only resident passerine species typical of mature forest habitats. For the Peruvian plot (Terborgh et al. 1990, Appendix), I deleted vagrant (V), edge (E), early successional (ES), and lake edge species (LS), as well as migrants (MG). Species associated with forest streams (ST) and tree fall openings (TF), as well as other classes of birds, were retained. Densities were reported as pairs per 100 ha. Species with densities too low to measure (+) were assigned 0.1 pair per 100 ha. The resulting sample included 126 species and 586.4 pairs per 100 ha.

For the French Guianian site, all the passerine species listed by Thiollay (1994, Appendix) were included except the migratory *Vireo olivaceus*. For two species of antbirds (*Federickena viridis* and *Pygiptila stelleris*), whose abundances were not estimated (+), I included 0.1

pairs/100 ha. The census included 146 species of passerines and 657.45 individuals per 100 ha.

Assuming that the census plots in French Guiana and Peru (roughly 600 pairs per 100 ha [1 km^2]) are representative of the densities of passerine birds in tropical forests in South America, we can estimate the total number of breeding pairs in all of South America by multiplying the total area of tropical forest in km^2 by 600. According to the United Nations Environmental Program, the combined area in South America of tropical lowland evergreen broadleaf rain forest (forest type 14) and semi-evergreen moist broadleaf forest (18) exceeds $5 \times 10^6 \text{ km}^2$ (data available online).² Thus, we may estimate the number of forest passerine birds in lowland, tropical South America as $600 \times 5 \times 10^6 = 3.0 \times 10^9$ breeding pairs, or approximately six billion breeding adult individuals.

The total South American passerine avifauna includes 1725 species (Meyer de Schauensee 1966). If, generously, tropical forest habitats harbor 1500 of these, the average population size would be $N = 4 \times 10^6$ individuals, and the estimated average time to extinction ($2N$, in generations) would be 40×10^6 Ma, assuming five years per generation. This exceeds, by more than an order of magnitude, values of 1.4 or 2.9 Ma estimated above from genetic divergence and lineage-through-time plots.

European birds

Population sizes for European birds have been estimated from extensive atlas projects in most countries, which are summarized in the EBCC Atlas of European Breeding Birds (Hagemeijer and Blair 1997). Estimates are presented as the total number of breeding pairs in Europe, European Russia (west of the Ural Mountains), and Turkey. The database includes 196 species of passerine birds, most of which are distributed generally through continental Europe. The total estimated number of pairs of all species is 1 417 824 413 (1.4×10^9) spread over roughly $10.5 \times 10^6 \text{ km}^2$. The maximum was for the Chaffinch *Fringilla coelebs*, estimated to have 120×10^6 pairs, but population estimates for an additional 33 species exceeded 10×10^6 pairs, and the average population size was 7.2×10^6 pairs.

Average adult mortality rates for temperate passerine birds are on the order of $M = 0.50$ (Henny et al. 1970, Dobson 1990, Karr et al. 1990) and, assuming birds begin to breed at an age of 1 year, the average generation time would be about $1 + 1/M = 3$ yr. Thus, for an average population size of 7.2×10^6 pairs (14.4×10^6 individuals), the expected time to extinction in a random drift model ($2N$ generations) would be more than 86×10^6 yr. This estimate for the average European population clearly is incompatible with intervals between extinction events. Drift is simply too slow to

² (http://www.unep-wcmc.org/forest/s_america_stats.htm)

account for the rates of turnover of passerine birds in either tropical or temperate communities.

DISCUSSION

As Leigh (1981) and Leigh et al. (1993) have pointed out, a critical test of individual-based neutral ecological theory is whether observed life spans of newly formed species are consistent with random drift in population size. The average time to extinction in generations should be on the order of twice the population size, as is the time for a population to increase from a small number to its present size (Leigh 1981). Extinction times are exponentially distributed (Grimm and Wissel 2004), and so their standard deviation is equal to the mean and many individual times to extinction would be several multiples of the average value. Calculations based on forest trees (Ricklefs 2003) suggested that drift is too slow to account for the turnover of species within a regional flora and that other forces must act. Observations on rapid increase in populations of introduced species, and relatively rapid decline in species richness in communities in recently isolated areas (Leigh et al. 1993, Ricklefs 2003), also do not support extinction by drift. As shown by the present analysis, even for passerine bird populations of average size expected times to extinction under drift greatly exceed values calculated from genetic divergence times and lineage-through-time plots. The expected persistence of the largest populations under a drift scenario would exceed the age of the passerine radiation.

Is it possible to extract oneself from this impasse and still cling to a neutral world? I believe there is no way around the fundamental problem for ecological drift—the problem of time.

What view of communities should we adopt?

Hubbell's (2001) view of ecology is individual based, recognizing that the geographic extent and abundance of a species reflect the demographic history of its population. Because every population must have an origin, Hubbell also emphasizes the fundamental importance of species origination. Although Hubbell's world is ecological in the sense that the total number of individuals is limited, individuals are not distinguished ecologically. Thus, it is possible to treat the dynamics of communities as random population processes, with limited dispersal providing some degree of spatial structure. Such a zero-sum ecological drift model produces as an outcome a stochastic statistical distribution of species abundances and extents. Age, rate of speciation, and area are defining components of both regional and local diversity in an ecological drift model (Kirkpatrick and Barton 1997, Butlin et al. 2003).

As many authors have pointed out, Hubbell's model is unrealistic because its basic premise of ecological neutrality of individuals is clearly not generally true, as shown by ecological segregation of species and density dependence within local areas. One can sidestep this difficulty to some extent by arguing that subsets of species match the

assumptions of an ecologically neutral model. However, assumptions about equilibrium also will rarely pertain in such cases; neutral communities of any size take too long to approach equilibrium relative to rates of climate and geomorphologic change, not to mention the evolutionary replacement of major lineages of species within communities. Finally, as I have emphasized here, observed turnover of species within regional pools occurs too rapidly to be accounted for by random stochastic processes. Individuals are too numerous for populations to disappear by drift in an empirically convenient time. Something else must be going on.

Ecological systems present us with a basic contradiction. On one hand, habitat selection and density dependence tend to establish demographic equality across species over regions and stabilize population sizes over time, so that changes in population size in a constant environment would proceed more slowly than predicted by drift. On the other hand, empirical evidence points to more rapid change than expected by drift. This contradiction can be resolved by two additional considerations. First, rapid changes in communities are commonly driven by extrinsic factors, such as climate change, whose characteristic times are much shorter than drift under most circumstances. Second, and perhaps less appreciated, coevolutionary interactions within ecological systems continually shift the demographic balance across species. These extrinsic and intrinsic drivers probably are responsible for changes in populations occurring at rates too fast to be accounted for by drift.

An important aspect of Hubbell's model is that both local and regional diversity are directly related to the rate of speciation within the metacommunity. Random processes combined with limited dispersal create a strong correlation between local and regional diversity. This has been observed empirically (see Srivastava [1999] for a review) but would seem to contradict the rapid approach to equilibrium of interacting populations within a classic, bounded, local community. This disparity in the relative strength of local compared to regional processes creates a difficulty for a regional perspective on local diversity (MacArthur 1965, Ricklefs 1987, 1989). I believe this difficulty has largely been created by the unrealistic and unmanageable concept of the community held, whether consciously or not, by most ecologists. Decades of empirical research have emphasized the openness of communities, with populations distributed more or less independently over multiple environmental gradients within large regions (Gleason 1926, Whittaker 1967, Cody 1993). In spite of this, community matrix models (Vandermeer 1972, May 1975), micro- and mesocosm experimental approaches in ecology (Morin 1999), and spatially constrained field studies of "communities" implicitly represent a locally bounded concept of the community, wherein populations interact with one another. Although this concept has been expanded by such

theoretical structures as metapopulations (Hanski and Gilpin 1997, Leibold et al. 2004), source-sink models (Pulliam 1988), landscape matrices (Forman 1999), and metacommunities with immigration dominating local communities (Loreau and Mouquet 1999, Hubbell 2001), these models essentially provide extended contexts for local, equilibrium ecological communities.

Many ecologists, including Hubble, have expanded their concepts of community to entire regions, within which populations are integrated by dispersal of individuals (e.g., Holt 1993, Loreau and Mouquet 1999, Leibold et al. 2004) and for which the diversity equation includes the rate of origination of new taxa. However, Hubbell's vision falls short to the extent that environments are not uniform within regions and species are not equivalent ecologically. Populations respond to each other and sort themselves out over environmental gradients by changes in local population density and geographic and ecological extent. The distribution of each species reflects its adaptations with respect to physical factors in the environment and biological agents. The latter are constantly changing through coevolution (Ricklefs 2004). Although the status of a particular species at a given time would be difficult to predict, its distribution through a region is more the product of deterministic processes of population interaction than of a random walk. Thus, we should think of ecological systems as being relatively stable with respect to parameters that change continuously.

Except for its abandonment of ecology, Hubbell's view of the world incorporates much of the regional and historical perspective that I would advocate. The fact that many ecologists have been attracted to this idea gives hope that the discipline is ready to embrace a more comprehensive concept of the species composition of ecological systems.

ACKNOWLEDGMENTS

Jerome Chave and Egbert Leigh generously commented on an earlier draft of the manuscript. Michel Loreau and several reviewers provided constructive guidance for preparing the final draft.

LITERATURE CITED

- Avise, J. C., and D. Walker. 1998. Pleistocene phylogeographic effects on avian populations and the speciation process. *Proceedings of the Royal Society of London, Series B, Biological Sciences* **265**:457–463.
- Boles, W. E. 1997. Fossil songbirds (Passeriformes) from the Early Eocene of Australia. *Emu* **97**:43–50.
- Brawn, J. D., J. R. Karr, and J. D. Nichols. 1995. Demography of birds in a Neotropical forest: effects of allometry, taxonomy and ecology. *Ecology* **76**:41–51.
- Brawn, J. D., J. R. Karr, J. N. Nichols, and W. D. Robinson. 1999. Demography of forest birds in Panama: how do transients affect estimates of survival rates? Pages 297–305 in N. J. Adams and R. H. Slotow, editors. *Proceedings of the 22nd International Ornithological Congress*, Durban. Bird-Life South Africa, Johannesburg, South Africa.
- Butlin, R. K., J. R. Bridle, and M. Kawata. 2003. Genetics and the boundaries of species' distributions. Pages 274–295 in T. M. Blackburn and K. J. Gaston, editors. *Macroecology: concepts and consequences*. Blackwell, London, UK.
- Chave, J. 2004. Neutral theory and community ecology. *Ecology Letters* **7**:241–253.
- Chave, J., and E. G. Leigh. 2002. A spatially explicit neutral model of beta-diversity in tropical forests. *Theoretical Population Biology* **62**:153–168.
- Clark, D. B., M. W. Palmer, and D. A. Clark. 1999. Edaphic factors and the landscape-scale distributions of tropical rain forest trees. *Ecology* **80**:2662–2675.
- Clark, J. S., and J. S. McLachlan. 2003. Stability of forest biodiversity. *Nature* **423**:635–638.
- Cody, M. L. 1993. Bird diversity components within and between habitats in Australia. Pages 147–158 in R. E. Ricklefs and D. Schluter, editors. *Species diversity in ecological communities: historical and geographical perspectives*. University of Chicago Press, Chicago, Illinois, USA.
- Condit, R. et al. 2002. Beta-diversity in tropical forest trees. *Science* **295**:666–669.
- Dobson, A. 1990. Survival rates and their relationship to life history traits in some common British birds. *Current Ornithology* **7**:115–146.
- Duivenvoorden, J. F., J. C. Svenning, and S. J. Wright. 2002. Ecology: beta diversity in tropical forests. *Science* **295**:636–637.
- Durrett, R., and S. Levin. 1996. Spatial models for species-area curves. *Journal of Theoretical Biology* **179**:119–127.
- Etienne, R. S., and H. Olf. 2004. A novel genealogical approach to neutral biodiversity theory. *Ecology Letters* **7**:170–175.
- Fisher, R. A. 1930. *The genetical theory of natural selection*. Clarendon Press, Oxford, UK.
- Fisher, R. A., A. S. Corbet, and C. B. Williams. 1943. The relation between the number of species and the number of individuals in a random sample of an animal population. *Journal of Animal Ecology* **12**:42–58.
- Fleischer, R. C., C. E. McIntosh, and C. L. Tarr. 1998. Evolution on a volcanic conveyor belt: using phylogeographic reconstructions and K-Ar based ages of the Hawaiian Islands to estimate molecular evolutionary rates. *Molecular Ecology* **7**:533–545.
- Forman, R. T. T. 1999. *Land mosaics: the ecology of landscapes and regions*. Cambridge University Press, Cambridge, UK.
- Gleason, H. A. 1926. The individualistic concept of the plant association. *Torrey Botanical Club Bulletin* **53**:7–26.
- Grimm, V., and C. Wissel. 2004. The intrinsic mean time to extinction: a unifying approach to analysing persistence and viability of populations. *Oikos* **105**:501–511.
- Hagemeijer, W. J. M., and M. J. Blair. 1997. *The EBCC atlas of European breeding birds*. Poyser, London, UK.
- Hanski, I., and M. E. Gilpin, editors. 1997. *Metapopulation biology: ecology, genetics, and evolution*. Academic Press, San Diego, California, USA.
- Harrison, G. L., P. A. McLenachan, M. J. Phillips, K. E. Slack, A. Cooper, and D. Penny. 2004. Four new avian mitochondrial genomes help get to basic evolutionary questions in the Late Cretaceous. *Molecular Biology and Evolution* **21**:974–983.
- Harvey, P. H., R. M. May, and S. Nee. 1994. Phylogenies without fossils. *Evolution* **48**:523–529.
- Henny, C. J., W. S. Overton, and H. M. Wight. 1970. Determining parameters for populations by using structural models. *Journal of Wildlife Management* **34**:690–703.
- Holt, R. D. 1993. Ecology at the mesoscale: the influence of regional processes on local communities. Pages 77–88 in R. E. Ricklefs and D. Schluter, editors. *Species diversity in ecological communities: historical and geographical perspectives*. University of Chicago Press, Chicago, Illinois, USA.
- Hubbell, S. P. 1979. Tree dispersion, abundance and diversity in a tropical dry forest. *Science* **203**:1299–1309.

- Hubbell, S. P. 2001. The unified neutral theory of biodiversity and biogeography. Princeton University Press, Princeton, New Jersey, USA.
- Hudson, R. R. 1990. Gene genealogies and the coalescent process. Pages 1–44 in D. Futuyma and J. Antonovics, editors. Oxford surveys in evolutionary biology. Oxford University Press, New York, New York, USA.
- Johns, G. C., and J. C. Avise. 1998. A comparative summary of genetic distances in the vertebrates from the mitochondrial cytochrome b gene. *Molecular Biology and Evolution* **15**:1481–1490.
- Johnson, N. K., and C. Cicero. 2004. New mitochondrial DNA data affirm the importance of Pleistocene speciation in North American birds. *Evolution* **58**:1122–1130.
- Johnston, J. P., W. J. Peach, R. D. Gregory, and S. A. White. 1997. Survival rates of tropical and temperate passerines: a Trinidadian perspective. *American Naturalist* **150**:771–789.
- Karr, J. R., J. D. Nichols, M. K. Klimkiewicz, and J. D. Brawn. 1990. Survival rates of birds of tropical and temperate forests: will the dogma survive? *American Naturalist* **136**:277–291.
- Kimura, M. 1983. The neutral theory of molecular evolution. Cambridge University Press, Cambridge, UK.
- Kimura, M., and T. Ohta. 1971. Theoretical aspects of population genetics. Princeton University Press, Princeton, New Jersey, USA.
- Kirkpatrick, M., and N. H. Barton. 1997. Evolution of a species' range. *American Naturalist* **150**:1–23.
- Klicka, J., and R. M. Zink. 1997. The importance of recent ice ages in speciation—a failed paradigm. *Science* **277**:1666–1669.
- Leibold, M. A., M. Holyoak, N. Mouquet, P. Amarasekare, J. M. Chase, M. F. Hoopes, R. D. Holt, J. B. Shurin, R. Law, D. Tilman, M. Loreau, and A. Gonzalez. 2004. The metacommunity concept: a framework for multi-scale community ecology. *Ecology Letters* **7**:601–613.
- Leigh, E. G. 1981. The average lifetime of a population in a varying environment. *Journal of Theoretical Biology* **90**:213–239.
- Leigh, E. G., S. J. Wright, and E. A. Herre. 1993. The decline of tree diversity on newly isolated tropical islands: a test of a null hypothesis and some implications. *Evolutionary Ecology* **7**:76–102.
- Loreau, M., and N. Mouquet. 1999. Immigration and the maintenance of local species diversity. *American Naturalist* **154**:427–440.
- Lovette, I. J. 2004. Mitochondrial dating and mixed support for the “2% rule” in birds. *Auk* **121**:1–6.
- MacArthur, R. H. 1965. Patterns of species diversity. *Biological Reviews* **40**:510–533.
- Magurran, A. E. 1988. Ecological diversity and its measurement. Princeton University Press, Princeton, New Jersey, UK.
- May, R. M. 1975. Stability and complexity in model ecosystems. Second edition. Princeton University Press, Princeton, New Jersey, USA.
- Mayr, G., and A. Manegold. 2004. The oldest European fossil songbird from the early Oligocene of Germany. *Naturwissenschaften* **91**:173–177.
- McGill, B. J. 2003. A test of the unified neutral theory of biodiversity. *Nature* **422**:881–885.
- Meyer de Schauensee, R. 1966. The species of birds of South America with their distribution. Academy of Natural Sciences, Philadelphia, Pennsylvania, USA.
- Morin, P. 1999. Community ecology. Blackwell Science, Oxford, UK.
- Pielou, E. C. 1969. An introduction to mathematical ecology. Wiley, New York, New York, USA.
- Pitman, N. C. A., J. W. Terborgh, M. R. Silman, P. Nunez, D. A. Neill, C. E. Ceron, W. A. Palacios, and M. Aulestia. 2001. Dominance and distribution of tree species in upper Amazonian terra firme forests. *Ecology* **82**:2101–2117.
- Potts, M. D., P. S. Ashton, L. S. Kaufman, and J. B. Plotkin. 2002. Habitat patterns in tropical rain forests: a comparison of 105 plots in Northwest Borneo. *Ecology* **83**:2782–2797.
- Potts, M. D., S. J. Davies, W. H. Bossert, S. Tan, and M. N. N. Supardi. 2004. Habitat heterogeneity and niche structure of trees in two tropical rainforests. *Oecologia* **139**:446–453.
- Pulliam, H. R. 1988. Sources, sinks, and population regulation. *American Naturalist* **132**:652–661.
- Ricklefs, R. E. 1987. Community diversity: relative roles of local and regional processes. *Science* **235**:167–171.
- Ricklefs, R. E. 1989. Speciation and diversity: integration of local and regional processes. Pages 599–622 in D. Otte and J. A. Endler, editors. Speciation and its consequences. Sinauer Associates, Sunderland, Massachusetts, USA.
- Ricklefs, R. E. 1997. Comparative demography of New World populations of thrushes (*Turdus* spp.). *Ecological Monographs* **67**:23–43.
- Ricklefs, R. E. 2003. A comment on Hubbell's zero-sum ecological drift model. *Oikos* **100**:185–192.
- Ricklefs, R. E. 2004. A comprehensive framework for global patterns in biodiversity. *Ecology Letters* **7**:1–15.
- Shields, G. F., and A. C. Wilson. 1987. Calibration of mitochondrial DNA evolution in geese. *Journal of Molecular Evolution* **24**:212–217.
- Sibley, C. G., and J. E. Ahlquist. 1990. Phylogeny and classification of the birds of the world. Yale University Press, New Haven, Connecticut, USA.
- Srivastava, D. 1999. Using local-regional richness plots to test for species saturation: pitfalls and potentials. *Journal of Animal Ecology* **68**:1–16.
- Terborgh, J., S. K. Robinson, T. A. Parker, III, C. A. Munn, and N. Pierpont. 1990. Structure and organization of an Amazonian forest bird community. *Ecological Monographs* **60**:213–238.
- Thiollay, J.-M. 1994. Structure, density and rarity in an Amazonian rainforest bird community. *Journal of Tropical Ecology* **10**:449–481.
- Tuomisto, H., and K. Ruokolainen. 1994. Distribution of Pteridophyta and Melastomataceae along an edaphic gradient in an Amazonian rain forest. *Journal of Vegetation Science* **5**:25–34.
- Tuomisto, H., K. Ruokolainen, R. Kalliola, A. Linna, W. Danjoy, and Z. Rodriguez. 1995. Dissecting Amazonian biodiversity. *Science* **269**:63–66.
- Vandermeer, J. H. 1972. Niche theory. *Annual Review of Ecology and Systematics* **3**:107–132.
- van Tuinen, M., and S. B. Hedges. 2001. Calibration of avian molecular clocks. *Molecular Biology and Evolution* **18**:206–213.
- Volkov, I., J. R. Banavar, S. P. Hubbell, and A. Maritan. 2003. Neutral theory and relative species abundance in ecology. *Nature* **424**:1035–1037.
- Whittaker, R. H. 1967. Gradient analysis of vegetation. *Biological Reviews of the Cambridge Philosophical Society* **42**:207–264.
- Wills, C., R. Condit, R. B. Foster, and S. P. Hubbell. 1997. Strong density- and diversity-related effects help to maintain tree species diversity in a neotropical forest. *Proceedings of the National Academy of Sciences (USA)* **94**:1252–1257.