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Neutral theory: a historical perspective

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Abstract

To resolve a panselectionist paradox, the population geneticist Kimura invented a neutral theory, where each gene is equally likely to enter the next generation whatever its allelic type. To learn what could be explained without invoking Darwinian adaptive divergence, Hubbell devised a similar neutral theory for forest ecology, assuming each tree is equally likely to reproduce whatever its species. In both theories, some predictions worked; neither theory proved universally true. Simple assumptions allow neutral theorists to treat many subjects still immune to more realistic theory. Ecologists exploit far fewer of these possibilities than population geneticists, focussing instead on species abundance distributions, where their predictions work best, but most closely match non-neutral predictions. Neutral theory cannot explain adaptive divergence or ecosystem function, which ecologists must understand. By addressing new topics and predicting changes in time, however, ecological neutral theory can provide probing null hypotheses and stimulate more realistic theory.

Introduction

To resolve what he thought was a paradox in panselectionism, Kimura (1968a) proposed a neutral theory of population genetics. Here, all genotypes have equal fitness: the only causes of change in allele frequencies are mutation, migration and demographic stochasticity. This theory provided a unifying frame for earlier studies of Wright (1931), Malécot (1948), Kimura (1955), Karlin & McGregor (1964, 1967) and many others. It evoked hostility (Ohta & Gillespie, 1996), but also stimulated elegant and creative mathematics (Ewens, 1972; Karlin & McGregor, 1972; Nagylaki, 1974, 1976; Watterson, 1974a,b, 1976, 1984; Kingman, 1977, 1978, 1982; Sawyer, 1977a,b, 1979; Sawyer & Fleischmann, 1979; Donnelly, 1986; Donnelly & Tavaré, 1987, 1995; Hoppe, 1987).

To learn whether species–area curves and species abundance distributions can be explained without invoking differences among species, Hubbell (1979, 1997, 2001), following an earlier attempt by Caswell (1976), constructed a neutral theory of forest dynamics and diversity. Here, a tree's species does not affect its prospects of death or reproduction. Hubbell modelled this theory on the neutral population genetics of a single multi-allelic locus in a haploid population. Neutral theory rewarded Hubbell, as it had Kimura, with abundant controversy, and with a variety of quantitative predictions, some in accord with observation. Theories that included more biology seemed unable to match these neutral predictions in an unforced manner.

Hubbell (2001), however, was a best-seller, whereas Kimura (1983) was not, even though Kimura's theory may prove more useful (Nee, 2005). Why were their receptions so different? What does this difference reveal about ecology compared with population genetics, and about the prospective contribution of neutral theory to each? To answer, I will:

1. review selected questions posed about neutral processes in population genetics, including Kimura's neutral theory, and the reasons for posing them;
2. outline those techniques for studying neutral processes in population genetics that allow the clearest and simplest presentation of Hubbell's neutral theory;
3. outline the motives and achievements of Hubbell's (2001) neutral theory of forest ecology, with special attention to its successful predictions;
4. discuss criticisms of Hubbell's neutral theory, evaluate its weaknesses and strengths, and suggest explanations for the contrasting reception of neutral theory in population genetics and ecology;

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5 suggest ways to expand this theory's scope and effectiveness, and outline its potential contributions to forest ecology.

Neutral theory in population genetics: the questions

This section outlines investigations concerning neutral processes in genetics from 1922 to their culmination in Kimura's (1968a, 1983) neutral theory. What questions were asked? Why were they asked? The presentation will emphasize questions relevant to the neutral theory of forest ecology; so, it focuses on infinite-allele models for a single locus in a haploid population. Despite the extensive study of neutral processes and the enormous body of techniques developed for this study, no population geneticist, not even Kimura, sought to deny the importance of adaptive evolution. Instead, all major workers were interested, at least to some degree, in how neutral processes affected adaptive evolution. Wright (1932) and Kimura (1983) even asked how neutral processes might rearrange genetic variation in ways that facilitate adaptive evolution.

Ronald Fisher asked questions, and developed techniques, relevant to the neutral theory to understand the origin of adaptation more clearly. Fisher (1922, 1930:73–76) used generating functions to calculate the prospects of survival and spread of a neutral mutation, because chance is the decisive influence on an allele's prospects when its numbers are few. Fisher (1958:84–87) also used generating functions to show that if a neutral mutant with a single bearer at generation 0 survived to generation n, it would have probability $\exp(-2j/n)$ of being represented then by more than j individuals. He concluded that chance would take unrealistically long to spread a neutral mutant through a large population. Fisher (1922, 1930) also showed that, absent mutation and selection, genetic variation in large populations declines so slowly that mutation is too rare to dictate the direction of evolution. Finally, Fisher (1930) argued that sexual reproduction evolved to enable the simultaneous fixation of new favourable mutations that first occur in different individuals of a population. This explanation presupposes finite populations and the role of chance in the spread of new mutations, but it focuses on adaptation. Fisher's studies of neutral processes were essential parts of his theory of adaptation by natural selection.

Sewall Wright also investigated neutral processes to understand the origin of adaptation. Wright (1932) believed that a genotype's fitness could not be accurately estimated from the average fitnesses of its component genes. He concluded that many populations would have to cross an 'adaptive valley' of lower fitness to attain higher fitness. Such crossings could only occur by chance. He therefore believed that adaptive evolution occurred most readily in large populations divided into many subpopulations that exchanged occasional migrants. In each subpopulation, allele frequencies would undergo 'genetic drift', leading to the formation of new genotypes. When an especially favourable genotype spread through a subpopulation, migrants would export it to the rest of the species (Wright, 1932). Wright (1931) therefore studied neutral processes to learn how they affect the occurrence of new gene combinations. To this end, he calculated the probability density of possible frequencies of a neutral allele in a subpopulation where immigration and mutation are in balance with genetic drift. This calculation enabled him to learn how low the rate m of exchange of migrants must be to allow significant differentiation among subpopulations (Wright, 1931:127–128).

Although population geneticists including Kimura (1955) had already treated a variety of neutral processes, Kimura only proposed his neutral theory in 1968 (Kimura, 1968a). He did not deny adaptation. Rather, he invented the neutral theory to circumvent an apparent paradox. Haldane (1957) had calculated that the spread by natural selection of an allele of initial frequency $q(0)$ through a population of constant size N would cost $N \ln[1/q(0)]$ selective deaths that would not have occurred were this allele substituted instantly. Kimura (1968a, 1983:25–26) proposed his neutral theory when he learned that a population experiences a nucleotide substitution every 2 years: he thought no population could support the mortality that these substitutions would impose were they driven by selection. Inventing the neutral theory, however, brought surprising rewards. In 1969, Kimura told me that the neutral theory was the first theory to allow him to make interesting, testable, seemingly valid, predictions in population genetics. Lewontin (1974) also noticed the difficulties of extracting useful predictions from non-neutral population genetics, but he did not become a neutral theorist.

Kimura's primary achievement in neutral theory was to show that a population's rate of neutral evolution is independent of its size. In a population of N adults, a new mutation carried by a single adult has frequency $1/N$. Its 'expected' future frequency is $1/N$: it either disappears, with probability $1 - 1/N$, or takes over the population, with probability $1/N$. If u new mutations occur per individual, Nu occur per generation of N individuals, of which u will be fixed. Therefore, the mutation rate per individual is the substitution rate per population (Kimura, 1968a). This achievement was the theoretical basis for the 'molecular clock' (Zuckerkandl & Pauling, 1965). Where the rate of molecular evolution is constant (clock-like), an easily understood, easily applied technique for inferring molecular phylogenies, the unweighted pair group method with arithmetic mean (UPGMA) is trustworthy (Nei, 1987:293–298; Felsenstein, 2004:161–166). The 'molecular clock' was a principal target for critics of the neutral theory (Gillespie, 1986).

Kimura & Crow (1964) considered the balance between mutation and random extinction at a single locus in a population of N haploids, where successive generations are distinct, each adult has probability u of carrying a new mutation and each new mutation is a new allele. Here, the probability F that two adults, sampled with replacement, carry the same allele is $1/(1 + 2Nu)$. Moreover, the expected number of alleles with frequency between q and $q + \mathrm{d}q$ is $\phi(q)\mathrm{d}q = 2Nu(1 - q)^{2Nu-1}\mathrm{d}q/q$ (Kimura & Crow, 1964:731, Kimura, 1968b:252).

Finally, Kimura & Ohta (1969:765) showed that in a population of N haploid adults, a new immutable mutant now carried by a single adult would take an average of $2N$ generations to spread through the population, if it is lucky enough to do so. If it is now carried by j adults, it takes an average of $2(N/j)(N - j)\ln[N/(N - j)]$ generations to spread through the population, if it is lucky enough to do so.

Since, Kimura's neutral theory has proved valid for 'third position' nucleotides with no effect on amino acid sequences (Ohta & Gillespie, 1996). It has also become a source of increasingly subtle null hypotheses by which to test for the presence of natural selection (Hartl & Clark, 1997:316; Nielsen, 2001). Subjects of these tests range from genome-wide phenomena (Bernardi, 2007) to the interplay of linkage, mutation and random drift at nearby sites along a DNA sequence (Sabeti *et al.*, 2002).

Neutral theory in population genetics: useful techniques

This section outlines techniques that simplify the analysis of neutral processes at single loci in haploid populations, first studied by other methods. I illustrate techniques inspired by Moran (1962) and Malécot (1948) that allow clearer presentation of the basic theses of the neutral theory of forest ecology and make its further development easier.

Models of populations with overlapping generations, especially Moran's (Moran, 1962:78–81; Ewens, 2004:104–109), are much easier to solve than models where successive generations are distinct. To see how such models simplify neutral theory, consider a multi-allelic locus in a panmictic population with N haploid adults. There are N time-steps per generation (the time required for N adults to die). Every time-step, let an adult be chosen at random to die, and another, which might (in contrast to the model of Hubbell, 1979) be the same one, to provide the gene at our locus for the instantly maturing replacement (hereafter, we say, 'provide the replacement young') for the dying adult. Finally, let each adult have probability $u \ll 1$ of bearing a new allele.

Moran and the steady-state distribution of genes over alleles

Let $\phi(j)$ alleles be represented by j genes apiece. What is the value of $\phi(j)$ at steady state? The probability $P(1,0)$ that the only carrier of its allele dies at the next time-step, and either does not reproduce, or replaces itself with a mutant young, is $1(N - 1 + u)/N^2 \approx (N - 1)/N^2$, whereas the probability that a new allele is born at that time-step is u. At steady state, $u \approx \phi(1)(N - 1)/N^2$, $\phi(1) \approx uN^2/(N - 1)$. The probability $P(j,j - 1)$ that one of the j bearers of an allele dies at the next time-step and is replaced by the bearer of another allele is nearly $j(N - j)/N^2$; the probability $P(j - 1,j)$ that one of an allele's $j - 1$ bearers produces a nonmutant young then, replacing a bearer of another allele, is $(j - 1)(N - j + 1)(1 - u)/N^2$. At steady state, the number $\phi(j - 1)P(j - 1,j)$ of alleles with membership increasing from $j - 1$ to j balances the number $\phi(j)P(j,j - 1)$ with membership decreasing from j to $j - 1$. As $\phi(j - 1)P(j - 1,j) = \phi(j)P(j,j - 1)$,

$$\begin{aligned}\phi(j) &= P(j-1,j)\phi(j-1)/P(j,j-1)\\ &\approx \phi(j-1)(j-1)(N-j+1)(1-u)/[j(N-j)],\\ \phi(2) &\approx \phi(1)(N-1)(1-u)/[2(N-2)]\\ &= uN^2(1-u)/[2(N-2)].\\ \phi(j) &= uN^2(1-u)^{j-1}/[j(N-j)].\end{aligned}$$

Let $uN/(1 - u) = \theta$. Then $\phi(j) = N\theta(1 - u)^j/[j(N - j)]$. Let $j \ll N$ (almost always true if $\theta \gg 1$) and set $j/N = x$, $1/N = q$, $\phi(j)/N = \Phi(q)\mathrm{d}q$. Then

$$\Phi(q)\mathrm{d}q = \theta(1-u)^{Nq}\mathrm{d}q/[q(1-q)] \approx \theta(1-q)^{Nu-1}\mathrm{d}q/q,$$

(Kimura & Crow, 1964:731). If $1 - u = x = N/(N + \theta)$ and $\theta = \alpha$, then

$$\phi(j) \approx \theta(1-u)^j/j = \alpha x^j/j, \tag{1}$$

the log-series of Fisher *et al.* (1943). In the Moran model, $\theta = uN/(1 - u)$ corresponds to Hubbell's (2001:121) fundamental biodiversity number.

The probability *F* that two genes are of the same allele, and its uses

Malécot (1948, 1969) showed that the behaviour of the probability $F(t)$ that two adults sampled from the same haploid population at generation t carry the same allele at a given locus is easily predicted. First, he showed how $F(t)$ changes in a population where alleles do not mutate ($u = 0$), successive generations are distinct and each generation has N reproductives. With probability $1/N$, two adults sampled from generation $t + 1$ inherit their gene from the same parent, so $F = 1$. With probability $1 - 1/N$ their genes come from different parents, so they have probability $F(t)$ of being the same allele. Therefore,

$$\begin{aligned}F(t+1) &= 1/N + (1-1/N)F(t), \quad 1 - F(t+1)\\ &= (1-1/N)[1-F(t)].\\ 1 - F(t) &= (1-1/N)[1-F(t-1)]\\ &= (1-1/N)^t[1-F(0)] \approx [1-F(0)]\exp(-t/N).\end{aligned}$$

(cf. Malécot, 1948:32; Crow & Kimura, 1970:101–102). 'Genetic drift' diminishes genetic variation, as measured by $1 - F$, but does so very slowly, at a rate inversely proportional to population size, as Fisher (1922, 1930) first showed.

Now let generations overlap according to the Moran model. Here, one adult dies at each time-step (each $1/N$ generation) and is immediately replaced by the instantly maturing young of an adult randomly chosen from the N alive just before the aforementioned adult died. Sample two adults at time t. With probability $1 - 2/N$, neither dies by time $t + 1/N$. If one dies, and if alleles do not mutate, its replacement has probability $1/N$ of inheriting its gene from the survivor. Here,

$$\begin{aligned} F(t+1/N) &= F(t)(1-2/N) + (2/N)[1/N \\ &\quad + (1-1/N)F(t)] = F(t) + 2[1-F(t)]/N^2, \\ 1 - F(t+1/N) &= [1-F(t)][1-2/N^2] \\ &= [1-F(1/N)][1-2/N^2]^{Nt} \\ &\approx [1-F(1/N)]\exp(-2t/N) \end{aligned}$$

(cf. Leigh *et al.*, 1993, 2004a; Gilbert *et al.*, 2006). Genetic drift diminishes $1 - F$ twice as fast in populations where generations overlap.

Now let each adult have probability u of bearing a new mutation at our locus. If generations overlap according to the Moran model, what is the equilibrium probability F that two adults sampled from a population of N bear the same allele? These adults' genes must have a common ancestor, and F is the probability that no mutation occurred in the line of descent of either gene since their latest common ancestor. Sample two adults at time t. The probability that one descended unmutated from the other at the last time-step is $(1 - u)/2N^2$, and the probability that one arose as a mutant then is $2u/N$. If neither happened then, the probabilities of these two events are the same for the time-step next before, and so forth. The probability F that these genes' latest common ancestor lived after the last mutation in their ancestry is thus (Ewens, 2004:329, 339–340)

$$\begin{aligned} [2(1-u)/N^2]/[2u/N + 2(1-u)/N^2] &= (1-u)/(Nu+1-u) \\ &= 1/[1+Nu/(1-u)]. \end{aligned}$$

If we set $Nu/(1 - u) = \theta$ (Ewens, 2004:294), then $F = 1/(1 + \theta)$.

If successive generations are distinct, the probability that one of our adults is a new mutant is nearly $2u$, the probability that their alleles are inherited unmutated from the same parent is $(1 - u)^2/N$, and

$$F \approx (1/N)/(2u + 1/N) = 1/(1 + 2Nu) \qquad (2)$$

(cf. Malécot, 1948:34–35; Kimura & Crow, 1964; Gillespie, 2004:46–47). Here, as in Hubbell (2001:121), the fundamental biodiversity number θ is $2Nu$ and $F = 1/(1 + \theta)$.

Next, what is the average number $k(n)$ of alleles in a sample of n adults? Again, let generations overlap, Moran style. Then $k(2) = 1 + \theta/(1 + \theta)$, for $\theta/(1 + \theta) = 1 - F$ is the probability that the second adult's allele differs from the first's. If n adults are sampled at one time-step, the probability that, at the last time-step, one inherited its allele unmutated from one of the $n - 1$ others is $n(n - 1)(1 - u)/N^2$, whereas the probability that one was born as a mutant then is nu/N. Reasoning as before, the probability that a new mutant arose since the most recent common ancestor of any pair of our alleles, which is $k(n) - k(n - 1)$, is $(nu/N)/[nu/N + n(n - 1)(1 - u)/N^2] = \theta/[1 + (n - 1)\theta]$ (Ewens, 2004:306–307). Thus $k(n)$, the expected number of alleles in a sample of n adults, is

$$\theta/\theta + \theta/(\theta+1) + \theta/(\theta+2) + \cdots + \theta/(\theta+n-1)$$

(Ewens, 2004:338–340). If n is large, $k(n) \approx \theta \ln[(\theta + n)/\theta] = \theta \ln[1 + n/\theta]$. If we set $\theta = \alpha$, the relation between the number n of adults sampled and the expected number k of alleles among them is predicted by the log-series (Fisher *et al.*, 1943; Watterson, 1974a).

Few species consist of one panmictic population. What happens in populations that exchange migrants with one or more others? First, consider a population of N adults where $u = 0$. Let each adult have probability m of being an immigrant from a large, panmictic source pool (as in Hubbell, 2001:83–86). Let the probability F^* that two members of the source pool carry the same allele be constant. F^* is also the probability that an immigrant has the same allele as a random adult in our population (Leigh *et al.*, 1993). At steady state, where the probability F that two adults sampled from our population have the same allele does not change, $F(t + 1/N) = F(t)$ is

$$\begin{aligned} F &= (1-2/N)F \\ &\quad + (2/N)\{mF^* + (1-m)[1/N + (1-1/N)F]\}, \\ F &= mF^* + (1-m)/N + (1-m)(1-1/N)F, \\ NmF &= NmF^* + 1 - m - (1-m)F, \\ F &= (NmF^* + 1 - m)/(Nm + 1 - m), \\ 1 - F &= Nm(1-F^*)/(Nm + 1 - m). \end{aligned} \qquad (3)$$

Populations with fewer immigrants (lower Nm) are more homozygous.

The probability that in a widespread, uniform population, two adults r km apart carry the same allele has long fascinated theorists (Wright, 1943, 1946; Malécot, 1948; Kimura & Weiss, 1964). To illustrate the method as simply as possible, consider a linear series of populations with N haploid adults apiece, which exchange migrants only with adjacent populations. Let each adult have probability u of carrying a new allele. How does the probability $F(n)$ that two adults from different populations separated by $n - 1$ intervening populations decline as n increases? Let generations overlap. Let each adult have probability $1 - m$ of inheriting its gene from its own population, probability $m/2$ of inheriting it from the population to its right, and equal probability of inheriting it from the population to its left. At steady state, let $F(0)$ be the probability that two adults from the same population carry the same allele, and let the probability that any two adults carry the same allele depend only on the distance between them. If $n > 1$, the probability that two adults n populations apart carry the same allele is

$$\begin{aligned}F(n) &= (1-2\mathrm{d}t)F(n) + 2\mathrm{d}t(1-u)\{m[F(n+1)\\ &\quad + F(n-1)]/2 + F(n)(1-m)\},\\ F(n) &= (1-u)\{F(n) + [F(n+1) - F(n)]m/2\\ &\quad - [F(n) - F(n-1)]m/2\}.\end{aligned}$$

Set

$$\begin{aligned}&F(n+1) - F(n) \approx \mathrm{d}F/\mathrm{d}n, \quad [F(n+1) - F(n)] - [F(n)\\ &\qquad - F(n-1)] \approx \mathrm{d}^2F/\mathrm{d}n^2.\end{aligned}$$

Then

$$\mathrm{d}^2F/\mathrm{d}n^2 \approx 2uF/m, \quad F(n) \approx F(0)\exp[-n\surd(2u/m)]. \quad (6)$$

The negative square root was chosen because F must decrease as n increases. Showing that $F(0)=1/[1+N\surd(2um)]$ (Chave & Leigh, 2002) is too difficult to do here.

This problem, or a close analogue, was solved for diploid populations where successive generations are distinct by Malécot (1969:81–84), Nagylaki (1974, 1976) and Sawyer (1977b). The two-dimensional case is more difficult to solve, but the methods for deriving the equation for F are the same (Chave & Leigh, 2002).

Branching processes, Moran style

Fisher (1930, 1958) used branching processes to study the initial spread of new mutations. He assumed that successive generations are distinct. Branching processes are simpler where an allele's bearers die one at a time. Consider a large population where an adult living at time t has probability $\mathrm{d}t$ of dying by time $t + \mathrm{d}t$ and equal probability of bearing an instantly maturing young by then (so time is measured in generations). If one adult carries an allele A at time 0 and A's do not mutate, what is the probability $p_k(t)$ that there are k A-bearers at time t? To answer, form the generating function

$$f_t(s) = \sum_{k=0}^{\infty} p_k(t)s^k$$

As different adults reproduce independently, $f_{t+w}(s) = f_t[f_w(s)]$. As $f_0(s) = s$ (there is one A when $t = 0$),

$$\begin{aligned}f_{\mathrm{d}t}(s) &= \mathrm{d}t + (1-2\mathrm{d}t)s + \mathrm{d}ts^2 = s + \mathrm{d}t(1-s)^2,\\ f_{\mathrm{d}t}[f_t(s)] &= f_{t+\mathrm{d}t}(s) = f_t(s) + \mathrm{d}t[1-f_t(s)]^2, f_{t+\mathrm{d}t}(s) - f_t(s)\\ &= \mathrm{d}f_t(s) = \mathrm{d}t[1-f_t(s)],\\ \mathrm{d}t &= \mathrm{d}\{1/[1-f_t(s)]^2\}, \quad t = 1/[1-f_t(s)] - 1/(1-s);\\ f_t(s) &= [t + s(1-t)]/[1+t-st].\end{aligned}$$

Here, $f_t(0) = t/(1 + t)$ is the probability that A has died out by time t (Feller, 1968: 480). Set $p_0(t) = E_t = t/(1 + t)$. Then the probability that A still survives at time t is

$$1 - E_t = 1/(1+t) \quad (4)$$

We may now set $f_t(s)$ equal to

$$\begin{aligned}&[E_t + (1-2E_t)s]/[1-E_ts] = E_t + (1-2E_t)s + E_t^2s\\ &\quad + E_t(1-2E_t)s^2 + E_t^3s^2 + \cdots\\ &\quad = t/(1+t) + [1/(1+t)]^2[s + ts^2/(1+t) + t^2s^3/(1+t)^2\\ &\quad + t^3s^4/(1+t)^3 + \cdots\end{aligned}$$

For every t, the expected number of A's is 1, so the expected number of A, given that the allele survives, is $1/[1 - p_0(t)] = 1 + t$. The probability $p_k(t)$ that there are k A's at time t is $t^{k-1}/(1 + t)^{k+1}$. If A's still survive, the probability is $t^{k-1}/(1 + t)^k$ that there are k A's then, and the probability that there are at least k A's then is $[t/(1 + t)]^{k-1}$. When $t \gg 1$,

$$[t/(1+t)]^{k-1} \approx \exp(-k/t). \quad (5)$$

If a neutral mutant survives so long, an average of k generations elapse before there are k A-bearers. If successive generations are distinct, however, the probability is $\exp(-2k/t)$ that a neutral mutant surviving to generation t has over k bearers then (Fisher, 1930).

Neutral theory of forest ecology: achievements

Having discussed the motives, techniques and achievements for studying neutral processes in population genetics, let us turn to Hubbell's (1979, 1997, 2001) neutral theory of forest ecology. The questions motivating this theory are: must we know how different species coexist to predict species abundance distributions or species–area curves (Hubbell, 2001: 6)? Are a plot's tree species present because they are the ones most suited to its microhabitats, or because they are the ones whose seeds happened to get there (niche assembly vs. dispersal assembly: Hubbell, 2001:8)? Here, there are two possibilities. Do too few seeds of a given species disperse from a large panmictic source pool to this plot to reach the microhabitats that best suit them, even though any seed could disperse across the source pool (Etienne & Alonso, 2005)? Or are seeds unable to reach the best microhabitats because they disperse only a limited distance from their parents?

Hubbell (2001:6–7) also considered the neutral theory as a 'teething ring' for theory with more biological content. Only recently did Hubbell (2006) suggest using the neutral theory as a null hypothesis.

Hubbell (2001) thought that the neutral theory explained species–area curves. His chapter on species–area curves, however, provided a quantitative prediction only for areas so small that panmixia applies. The log-series implies that the number S of species in a sample of N trees is $S = \alpha \ln(1 + N/\alpha)$, where α is Fisher's alpha (Fisher *et al.*, 1943). On some tropical forest plots ≤ 50 ha in area, this is nearly true (Condit *et al.*, 1996a, 2004). Caswell (1976) was the first ecologist to predict this relation from the neutral theory.

Bramson *et al.* (1996, 1998) essayed a neutral theory of species–area curves on a square lattice of trees, each a unit distance from its four nearest neighbours. Here, a tree alive at time t has probability $\mathrm{d}t$ of dying by time $t + \mathrm{d}t$. If it dies, each of its four nearest neighbours has probability 1/4 of being seed-parent of the replacement young, which has probability u of being a new species. Bramson *et al.* (1998) scale N relative to $1/u$, setting $N = (1/u)^y$, $\ln N = y \ln(1/u)$. If $u \ll 1$, $N \gg 1$, $Nu < 1$, then the number of species in a square of N contiguous trees is given by

$$S/N = u[y\ln(1/u)]^2/2\pi = u(\ln N)^2/2\pi; \quad S = Nu(\ln N)^2/2\pi,$$

(Bramson *et al.*, 1998, equation 1.3). If the mean square dispersal distance of offspring from parent is σ^2 rather than 1, then $S = Nu(\ln N)^2/2\pi\sigma^2$ (Chave *et al.*, 2002:20). Bramson *et al.* (1996) scale N relative to L^2, setting $N = L^{2r}$, where $L = 1/\sqrt{u}$, the distance a random-walking line of descent with unit step-length is likely to propagate across a lattice in $1/u$ time-steps before it mutates (Hubbell, 2001:174). If $N > 1/u$, then

$$S = 2Nu[\ln(1/\sqrt{u})]^2/\pi = Nu[\ln(1/u)]^2/2\pi$$

(Bramson *et al.*, 1996, equation 1.2). For L so large that a species rarely spreads so far before dying out, S increases linearly with N. No one, however, has yet derived the familiar species–individual curve, $S = cN^z$, where $z < 0.4$, (MacArthur & Wilson, 1967), from the neutral theory.

Although 50-ha plots have stimulated analyses of species–area curves (Condit *et al.*, 1996a, 2004; Plotkin *et al.*, 2000a,b), species–area curves have played a minor role in empirical discussions of the neutral theory, presumably because they offer much less support for it than, say, species abundance distributions. Accordingly, species–area curves will not be discussed further in this paper.

The most famous achievement of Hubbell's (1997, 2001) neutral theory is accounting for the distribution of trees ≥ 10 cm dbh over species on a 50-ha plot at Barro Colorado Island, Panama, assuming that a fraction m of its seed-parents were chosen from a large source pool, and assuming panmixia and neutral dynamics for both the plot and the source pool. This example will be examined in detail.

With neutral dynamics, the number of species represented by k trees apiece in a panmictic source pool with M trees and speciation rate u is $\phi(k) \approx (\alpha/k)(1 - u)^k$ (eqn 1). In the Moran model, $\alpha = Mu/(1 - u)$. Hubbell assumed that the plot's most common tree species were equally dense in the source pool. In the log-series best fitting these common trees, $\alpha = 50$. Setting $\alpha = 50$ for the source pool, and setting immigration rate $m = 0.1$ fit the species abundance distribution of trees ≥ 10 cm dbh on the plot.

Volkov *et al.* (2003) and McKane *et al.* (2004) provide an easily understood way to calculate the species abundance distribution of trees on a plot, given m and the source pool's α. The number $\psi(j)$ of species with j trees apiece on the plot is roughly

$$\sum_{k=j}^{M} \phi(k) P_k(j),$$

where M is the number of trees in the source pool, $\phi(k)$ is the number of species with k trees apiece in this pool, and $P_k(j)$ is the probability that a species with k trees in the source pool has j of the plot's N trees. If a species has k trees in the source pool, the probability that one of these trees is seed-parent to a tree on the plot at the next time-step is mk/M. Thus, if this species now has no trees on the plot, the probability $P_k(0,1)$ that it has one after the next time-step is mk/M. If this species now has one tree on the plot, the probability $P_k(1,0)$ that it dies at the next time-step and is replaced by some other species is $(1/N)[(1 - m)(N - 1)/N + m(M - k)/M)]$, where $1/N$ is the probability that the one tree on the plot of this species dies, $(1 - m)(N - 1)/N$ is the probability that it is replaced from the plot by another species, and $m(M - k)/M$ is the probability that it is replaced from the source pool by another species. At steady state, $P_k(0)P_k(0,1) = P_k(1)P_k(1,0)$, so $P_k(1) = P_k(0)P_k(0,1)/P_k(1,0)$. Similarly, $P_k(1)P_k(1,2) = P_k(2)P_k(2,1)$, so

$$P_k(2) = P_k(0)P_k(0,1)P_k(1,2)/P_k(1,0)P_k(2,1).$$

The calculation continues similarly for larger j, and is completed by setting $\sum_{j=0}^{N} P_k(j) = 1$. The calculation is inexact, because it assumes that the memberships of species on the plot change independently, whereas they must actually sum to N. Etienne (2005) provides more precise maximum-likelihood methods of calculating m and the source pool's α and the most probable distribution of species abundances on the plot.

Is the migration rate m estimated by this method more than an arbitrary fitted parameter? If each tree's seeds are distributed about their parent according to the same radially symmetric Gaussian, then $m = 0.1$ implies a root mean square dispersal distance from parent to offspring near 59 m (Leigh *et al.*, 2004a). H. C. Muller-Landau fit radially symmetric Gaussians to distributions of seeds about parent trees for 65 different species. Root mean square dispersal distance varied greatly from species to species, in violation of the neutral theory's assumptions, but the average over all species was 55 m (Condit *et al.*, 2002). Is this match of observation to prediction meaningful?

There is no such thing, however, as a panmictic source pool. To develop the neutral theory more reasonably, one must let seeds disperse only to a limited distance from their parents. Following Malécot (1948) and Nagylaki (1974), Chave & Leigh (2002) constructed a neutral theory of species turnover, assuming limited dispersal of seeds from parents. Consider a limitless forest with ρ trees per m^2, where each tree has probability u of being a new species, a tree alive at time t has probability dt of dying by time t + dt, and the probability is $\exp(-r^2/\sigma^2)$ that a dead tree is replaced by the immediately maturing young of a tree $< r$ m away, where σ is the root mean square distance from a tree to its young. Then, at steady state, the probability $F(r)$ that two trees r km apart belong to the same species is nearly

$$2K_0[(r/\sigma)\sqrt{u}]/[\pi\rho\sigma^2 + \ln(1/u)], \quad \text{if } r > \sigma$$

(Chave & Leigh, 2002). K_0 is the modified Bessel function of order 0: when $x > 3$, $K_0(x) \approx \sqrt{(\pi/2x)}\exp(-x)$ (Olver, 1965). Here, $x = r/L$, where $L = \sigma/\sqrt{u}$ is the distance a species is likely to spread before it dies out (Hubbell, 2001:174). Barro Colorado's plot has one tree ≥ 10 cm dbh per 23.3 m^2. If we set $\sigma = 57$ m, $u = 4.8 \times 10^{-8}$ and $1/\rho = 23.3$ m^2, the predicted $F(r)$ fits the trend of the data for trees ≥ 10 cm dbh on 1-ha sample plots over 100 m apart in central Panama (Condit *et al.*, 2002). To be sure, there was much scatter about this trend: species composition of plots on similar soils were more similar, and species composition of plots on very different soils were more different, than the neutral theory predicted (Condit *et al.*, 2002). The root mean square dispersal distance of 57 m calculated by Condit *et al.* (2002) to fit the species turnover data is close both to 55 m, the average of the root mean square dispersal distances calculated for tree species on Barro Colorado's plot by H. C. Muller-Landau (Condit *et al.*, 2002) and to the 59 m calculated by assuming that 10% of the trees on this plot have seed-parents outside it (Leigh *et al.*, 2004a). Does this mean that it is safe, for certain predictions at least, to assume panmictic source pools?

Evaluating Hubbell's neutral theory

Hubbell's (1979, 1997, 2001) neutral theory of forest ecology has aroused abundant controversy, as one might expect, for it ignores Darwin's (1859:110–116) concept of adaptive divergence of character (Alonso *et al.*, 2006). This concept was crucial to Darwin's (1859) explanation of diversity, as it was to Fisher's (1930:125–131), Lack's (1947), MacArthur's (1961, 1972), Mayr's (1963), Grant's (1986), Schluter's (2000), Mayr & Diamond's (2001) and many others. Neutral theorists' defence of a simple theory capable of useful quantitative prediction clashes with other biologists' pursuit of Darwin's approach. This section considers empirical objections to the neutral theory, and evaluates the theory's weaknesses and strengths.

Empirical objections to neutral theory

Empirical objections to the neutral theory fall under four heads. First, its fundamental axiom, that all trees are alike before natural selection regardless of their species, is false (Hubbell, 2001:6). Different species respond differently to environmental change (Condit *et al.*, 1996b). Different species adjust differently to the master trade-off between growing fast in bright light and surviving in shade (Brokaw, 1987; Pacala *et al.*, 1996; Wright *et al.*, 2003). Different species are adapted to different habitats (Fine *et al.*, 2004). Seedlings and saplings grow more slowly, and die more quickly, where conspecifics are more common (Harms *et al.*, 2000; Hubbell *et al.*, 2001). Most, if not all, of these differences reflect adaptive divergence. No one denies these facts, although some, such as Chave (2004:250–251), question their impact on the neutral theory's predictions.

The second category of criticisms stems from tests of 'common-sense' deductions from the neutral theory. Terborgh *et al.* (1996:563) assumed that floodplain forests separated by upland forest bluffs developed 'in the absence of spatial correlation' with each other, so that, in a neutral world, their species compositions would develop independently. Mature floodplain forests 30 km apart on the Río Manú, isolated from each other by 2 km of riverfront bluffs separating their floodplains, are unexpectedly similar in species composition and relative abundance of common species (Terborgh *et al.*, 1996). Patterns of succession from newly formed riverbank are also remarkably similar on these floodplains (Foster *et al.*, 1986; Salo *et al.*, 1986; Terborgh & Petren, 1991). These similarities are especially remarkable because the species composition of floodplain forest differ greatly from that of the upland forest separating one floodplain from another. Hubbell (2001:331) countered that seed dispersal maintained the homogeneity of the floodplain forests. Nonetheless, the similar patterns of successional development in these forests, and the striking differences between floodplain forest and adjoining upland forest, imply severe restrictions to the generality of the neutral theory.

Clark & McLachlan (2003) assumed that the neutral theory implies that the species composition of forests 50 km apart in a uniform landscape drift independently, and should therefore diverge progressively. Examining pollen records for the last ten thousand years in lakes scattered over 10 000 km^2, they found no evidence for progressive divergence in tree species composition, and declared the neutral theory falsified. Clark and McLachlan also cited *Tsuga canadensis*, which suddenly became rare over a million square kilometres over 5000 years ago, and recovered its former abundance after 1500 years, as if wasted by a new pathogen to which it later acquired immunity (Allison *et al.*, 1986). Hubbell & Foster (1986:322) had said that return to previous abundance after the cessation of an abundance-depressing disturbance is evidence against the neutral theory. *Tsuga* provides that evidence. In reply, Volkov *et al.* (2004), ignoring *Tsuga*, argued that dispersal can maintain the homogeneity of the forest over some (unspecified) distance. Neither Hubbell nor Volkov used the neutral theory to predict the homogenizing power of dispersal: that requires reckoning with the limited dispersal of seeds from their parents. Instead, both relied on the fictitious concept of a panmictic source pool, where seeds can disperse from one end to the other.

The third category of objections concerns neutral theorists' emphasis on species abundance distributions. Most neutral theory tests compare predicted species abundance distributions with those observed on 50-ha plots, especially Barro Colorado Island's plot. McGill's (2003) claim that a log-normal fit Barro Colorado's species abundance distribution better than Hubbell's simulations led to progressively more exact calculations (Volkov *et al.*, 2003; Etienne & Olff, 2004, 2005). The sampling theory of Etienne & Olff (2005) calculated most likely values of source pool α and immigration rate m from the source pool from a plot's species abundance distribution. These methods, however, could not judge decisively between Etienne and Olff's neutral theory prediction and the log-normal.

A simpler calculation predicts source pool α, given immigration rate m and the probability F that two trees ≥ 10 cm dbh in a plot with N trees are conspecific. If trees in the source pool are distributed over species in a log-series with $\alpha = \theta$ (eqn 1), the probability that two trees sampled from the source pool are conspecific is $1/(1+\theta)$. If a fraction m of the plot's N trees have seed-parents in the source pool, then, by eqn 3,

$$F = [Nm/(1+\theta) + 1 - m)]/(Nm + 1 - m).$$

On Barro Colorado's plot, $F = 1/(38.0)$ (calculated from 1995 census data supplied by Suzanne Lao from R. Condit and the Center for Tropical Forest Science). Here, if $m = 0.1$, then θ, the source pool's α, is 37.6; if $m = 0.093$, then $\theta = 37.65$. The most likely values of m and source pool α calculated from this 1995 census by Etienne's sampling theory are 0.093 and 47.7 respectively (Chave *et al.*, 2006). I do not know why these two methods give such different expectations for θ.

The parameter m in Etienne's species abundance distribution is, moreover, seldom measured, nor have neutral theorists compared estimates made by different methods. A rough calculation (Leigh *et al.*, 2004a:260–261) suggests that if $m = 0.093$ for a 50-ha plot, as Chave *et al.* (2006) report for Barro Colorado, then root mean square dispersal distance σ is 55 m, close to the 57 m that gives the best fit for species turnover near Barro Colorado (Condit *et al.*, 2002). The same rough calculation shows that if $\sigma = 77.5$ m, the value that best fits species turnover around Yasuni in Amazonian Ecuador (Condit *et al.*, 2002), then, for Yasuni's 25-ha plot, $m = 0.175$. Applying Etienne's estimator to the trees ≥ 10 cm dbh on the 25-ha plot at Yasuni yields a most likely value of 0.43 for m (Chave *et al.*, 2006). Is the fit for Barro Colorado fortuitous? As Ricklefs (2006:1426) remarks, proper test of a mechanistic theory involves more than curve-fitting.

Furthermore, a log-series distribution in the source pool does not necessarily imply neutral dynamics, as Gillespie (1991) pointed out for the neutral theory of population genetics. Gillespie's (1991) non-neutral explanation for the log-series has a parallel in ecology – tree species with identical mortality which coexist by temporally partitioning tree fall gaps: in different years, different species are most successful in occupying these gaps (Chesson & Warner, 1981; Hatfield & Chesson, 1989). Purves & Pacala (2005) found that a log-series distribution in the source pool does not imply the absence of strong non-neutral processes. Regrettably, MacArthur's (1966) skepticism concerning the usefulness of species abundance distributions has not been much heeded.

The fourth group of criticisms centres on tests of neutral predictions of changes in time. For example, Leigh (1981) showed that, according to the neutral theory, the average time to extinction of a population now containing N adults was more than N generations. Without assembling supporting data, he claimed that very common species do not last so long in the fossil record, and concluded that extinctions of such species must be caused by some change in their environment. Ricklefs (2003), who assembled supporting data, independently found that common species are shorter lived than the neutral theory predicts. Neutral predictions of changes in time often make good null hypotheses because falsifying them, unlike falsifying most neutral predictions of species abundance distributions (McGill *et al.*, 2006), often suggests alternate hypotheses which shed light on the ecological organization of tropical forests. Two such tests will be discussed.

The neutral theory predicts limits to how fast a tree population changes. If a tree species forms a small proportion of the forest, and if its trees die one by one, the number of its deaths should not differ more from the number of its recruitments than the number of heads from the number of tails in a corresponding number of tosses of a fair coin (cf. Gilbert *et al.*, 2006:307). Census data from Barro Colorado's 50-ha plot was provided by Suzanne Lao on behalf of R. Condit and the Smithsonian's Center for Tropical Forest Science. Barro

Colorado's 1985 census counted 1900 *Trichilia tuberculata* ≥ 10 cm dbh, of which 239 died by the 1990 census, which counted 1783 *T. tuberculata* ≥ 10 cm dbh. Therefore, 122 *T. tuberculata* recruited between 1985 and 1990 (1900 − 239 + 122 = 1783). If deaths and recruitments were equally likely, the expected number of deaths in this species between 1985 and 1990 would be (239 + 122)/2 = 180.5, and its standard deviation would be √(361/4) = 9.5. The number dying is over six standard deviations higher than predicted: the number of trees of this species declined *significantly* between 1985 and 1990. Similar reasoning shows that the numbers of trees ≥ 10 cm dbh of three of the plot's eight most common species (omitting the clonal palm *Oenocarpus mapora*, where deaths are difficult to ascertain) increased significantly during all four 5-year census intervals between 1985 and 2005, and two others decreased during every interval. For eight of the plot's 11 next most common species, the number of trees ≥ 10 cm dbh dying between 1985 and 2005 was in significant imbalance with the number of recruitments. During any one census interval, deaths were in significant imbalance with recruitment in at least 11 of these 19 species (Table 1). Changes differed significantly among these tree species. Hubbell & Foster (1990) emphasized the prevalent disequilibrium among trees on this plot, without comparing the magnitude of the change in populations of different tree species with neutral predictions.

The neutral theory also predicts how fast chance can spread a new tree species or clade, if it survives so long. *Ocotea* (Lauraceae) dispersed southward across the sea then separating North and South America, and *Symphonia globulifera* (Guttiferae) dispersed across the sea from Africa to South America, about 20 million years ago (Chanderbali *et al.*, 2001; Dick *et al.*, 2003). *S. globulifera* now averages more than one tree ≥ 10 cm dbh per hectare throughout Amazonia: South America must contain over 10 million reproductive adults of this species (Leigh *et al.*, 2004b:449). If annual mortality averages 2%, less than 500 000 tree generations have elapsed since this species invaded South America. If so few invaders reached adulthood that only one tree's chloroplasts has surviving descendants, eqn 5 implies that the probability that *Symphonia* multiplied so quickly by chance is about e^{-20}, or 2×10^{-9} (Leigh *et al.*, 2004b:448–449). The same applies to *Ocotea*. Other plants have also invaded Amazonia successfully. At least 20% of the 1000 free-standing woody species on a 25-ha plot in Amazonian Ecuador descend from invaders that crossed the sea after South America became an island continent (Pennington & Dick, 2004).

Table 1 Balance between death and recruitment in selected tree species on the 50-ha forest dynamics plot of Barro Colorado Island, Panama.

Species	N 85	D	N 90	D	N 95	D	N 00	D	N 05
Trichilia tuberculata	1900	†239	1783	†166	1681	†207	1572	†204	†1429
Faramea occidentalis	1400	*146	1649	*196	1717	*202	1828	*260	*1909
Poulsenia armata	857	†161	801	†134	755	†168	671	†128	†630
Alseis blackiana	854	*19	936	*15	981	*20	1013	*35	*1046
Quararibea asterolepis	694	38	699	*30	724	37	723	47	714
Gustavia superba	641	11	649	8	644	22	638	†30	619
Virola sebifera	587	46	605	46	615	†70	589	†84	559
Hirtella triandra	552	*33	618	*22	681	*37	717	*39	*765
Cordia lasiocalyx	445	47	444	†92	364	†91	295	†65	†248
Guarea guidonia	362	*16	376	18	376	29	370	24	359
Socratea exorrhiza	357	†64	336	41	346	†56	325	†56	†297
Protium tenuifololium	350	39	358	*21	381	23	392	30	*406
Tetragastris panamensis	330	*12	362	*21	379	*15	397	21	*399
Prioria copaifera	308	*7	335	13	344	12	352	7	*357
Beilschmiedia pendula	304	19	296	15	295	†20	282	†22	†270
Tabernaemontana arborea	303	24	304	*14	323	*15	341	*20	*362
Cordia bicolor	259	*16	285	*23	326	29	328	31	323
Heisteria concinna	255	*13	274	*7	288	16	288	22	*292
Cecropia insignis	246	40	257	32	263	*29	281	*41	*342

Numbers, *N*, of trees of each species in the census indicated, and the number *D* dying before the next census. Deaths are considered in significant imbalance with recruitment if, letting *D* be the number of deaths between censuses *t* and *t* + 1,

$$|N(t+1) - N(t)| > 2\sqrt{\{N(t+1) - N(t) + 2D\}}.$$

Deaths are considered in significant imbalance with recruitment if

$$|N(05) - N(85)| > 2\sqrt{\{N(05) - N(85) + 2\sum D\}},$$

where $\sum D$ is the sum of the deaths in this species occurring during each of the four census intervals. * before the number of deaths denotes a significant increase within the census interval, and † denotes a significant decrease. * before N 05 denotes a significant increase over the whole 20-year period, and † before N 05 denotes a significant decrease during this period.

Although their advantages spread these species all across Amazonia, no species makes up more than a small proportion of the forest: the invaders could not replace their predecessors. Tropical tree species must therefore differ in ways that allow a great many of them to coexist, with none able to replace the others, contra Huston (1994). Understanding tropical tree diversity requires learning what these differences are. This finding, which is crucial for future research directions, was revealed by using a null hypothesis from the neutral theory.

Weaknesses and strengths of neutral theory

Now that the neutral theory has been evaluated in empirical and historical context, it is time to sum up this theory's current weaknesses and strengths. One weakness of the neutral theory is the narrow range of its concerns – an extraordinary happenstance, considering the theory's justly vaunted potential for synthesis. Unlike population geneticists, ecological neutral theorists have ignored changes in time, failing to test whether neutral patterns are generated by neutral processes. They have abandoned the task of testing whether many pairs of species diverged simultaneously in response to a new barrier to their neutral counterparts in population genetics (Hickerson *et al.*, 2006). Most analytical neutral theorists have abjured spatially explicit theory. Chave & Leigh's (2002) spatially explicit theory of species turnover assumes a most implausible steady state: unlike the population geneticist Nagylaki (1974, 1976), no ecologist has considered the manner, or the speed, of approach to this steady state. With one exception (Chave *et al.*, 2002), analytical predictions of species–area curves, which require spatially explicit mathematics, have been left to professional mathematicians (Bramson *et al.*, 1996, 1998), whose derivations few biologists can understand.

Instead, ecological neutral theorists have focussed almost exclusively on species abundance distributions in plots that receive migrants from a panmictic source pool. They have fit predicted formulae to observed distributions of abundance (often very successfully) without trying to eliminate, or at least test the importance of, unrealistic auxiliary assumptions such as panmictic source pools. Only professional mathematicians, not read by biologists, have tried to derive species abundance distributions where young disperse only a limited distance from their parents (Bramson *et al.*, 1998). The probability u that a tree belongs to a new species, a fitted parameter, takes the place of a proper neutral theory of speciation. The values of u used to fit the 'species turnover' formula – the probability $F(r)$ that two trees r km apart are conspecific – to different data sets are unsettlingly different. The value of u fitted for central Panama is 1300 times the value fitted for Yasuni in Ecuadorian Amazonia and 2 600 000 times that for Manú in south-eastern Amazonian Peru (Condit *et al.*, 2002, legend to Fig. 2). The speciation rate u also appears in the fundamental biodiversity number $\theta = Nu$, another fitted parameter. As N is the number of trees in a fictitious panmictic source pool, the presence of u in the parameter θ sheds no additional light on speciation rate. Much work must be done to construct a truly testable neutral theory, free of confounding auxiliary assumptions (Dayton, 1973), that can generate trustworthy null hypotheses.

These weaknesses may not ruin all usefulness of current neutral models. Latimer *et al.* (2005) used the neutral theory to compare dispersal limitation and speciation rate among woody plants of the Cape fynbos with those among Amazonian trees. Unfortunately, this analysis treated a set of scattered plots as a single panmictic plot to calculate Nu for, and immigration rate m from, their source pool. Nonetheless, the authors' conclusion that speciation was far higher, and dispersal distances much shorter, in the fynbos than among Amazonian trees, is supported by empirical data. Surely, analysing these sets of plots by the methods of Condit *et al.* (2002) would have yielded the same conclusion with fewer questionable assumptions.

Again, nothing appears more ridiculous than assuming that each tree has probability u of being the first member of a new species. Hubbell (2001) explored the effects of replacing mutational speciation by the random splitting of populations. Etienne *et al.* (2007) assumed that (mutational) speciation rate within a species was inversely proportional to its population size, so that each species produced daughter species at the same rate. The 'standard model' of Hubbell (2001) and Etienne (2005) outperformed both alternatives. Indeed, it appears that most plant species descend from small, local populations (Leigh *et al.*, 2004b). If so, assuming that species start from single trees may not alter predictions of ecological interest. Equation 4 implies that a new species with a single tree has probability $1/n$ of having descendants n generations later. If $k \ll n$, the probability that a new species starting with k trees has no descendants n generations later is $(1 - 1/n)^k \approx \exp(-k/n) \approx 1 - k/n$. This species has probability $1 - \exp(-k/n) \approx k/n$ of surviving to that time. The probability that only one of the k founders has descendants in the female line then is

$$(k/n)(1 - k/n)^{k-1} \approx (k/n)\exp(-k/n).$$

The probability that, if this species survives to generation n, all members alive then descend in the female line from a single ancestor is $[(k/n)\exp(-k/n)]/[1 - \exp(-k/n)]$. If this is nearly 1, then the distribution of the number of descendants at generation n of a species starting with k trees, given that it still survives then, is the same as if the species had started with a single tree. Thus, if Nu adults belonging to new species are born into a source pool each generation, a plot's species abundance distribution should be the same whether these Nu adults belong to one species, Nu species, or any number in between, so long as every species on the plot has at least $n \gg Nu$ adults in the source pool.

Some weaknesses, however, will be harder to cure. Deriving spatially explicit theory of species–area curves or species abundance distributions for different scales, assuming that offspring disperse only a limited distance from their parents will not be easy. Despite Hubbell's breadth of vision, the neutral theory of forest ecology has yet to attract theoreticians with the nose for crucial problems and the mathematical skills to solve them of a Fisher, a Kimura, a Malécot or a Nagylaki. Nonetheless, if the interest and the promise of the neutral theory can be made clear without confusing it with truth, or even the truth of ideal-gas models, the theory should attract skilful workers.

The neutral theory's fundamental, unavoidable weakness is, of course, its false basic assumption. Differences between tree species matter. Ignoring these differences makes the neutral theory unable to treat ecosystem properties (Westoby & Wright, 2006). Moreover, founding the neutral theory on the irrelevance of species differences means that we cannot know in advance which of its predictions will work. Why does the neutral theory predict (some!) species abundance distributions so well, and species–area curves so poorly? Not knowing why this theory works where it does, we can never be sure to what new topics it can safely be applied. The neutral theory's false assumptions restrict its usefulness to:

1. domains where neutrality prevails, such as extinction from a plot of species represented there by one or two trees, or short-term fluctuations about equilibrium of a plot's tree species composition (Gilbert *et al.*, 2006);
2. first stabs at otherwise impenetrable topics, especially those requiring spatially explicit theory, such as species–area curves or species turnover;
3. predictions trancending the validity of the neutral theory's assumptions, that need more realistic derivations, such as species abundance distributions; and
4. employment as a null hypothesis.

The neutral theory wins adherents through its successful predictions, especially of species abundance distributions and, to a lesser extent, species turnover. These successes, however, depend on unmeasured parameters such as the speciation rate u and unrealistic assumptions such as panmictic source pools. Nonetheless, the neutral theory may enable economical summary, and perhaps even a workable method of interpolation, for many types of diversity data from extensive, species-rich forests such as Amazonia.

The neutral theory's fundamental and abiding strength, however, is the very simplicity of its assumptions. These simple assumptions allow the development of theory on topics such as species–area curves, phylogenetic patterns and species turnover, that are not otherwise amenable to precise, mechanistic theory. The neutral theory of species turnover has drawn attention to how the local origin and finite spread of different plant species contributes to species turnover (Leigh *et al.*, 2004a). The neutral theory may well make other such contributions in future. At the very least, ecological neutral theory, like that in population genetics, provides natural, yet probing null hypotheses with which one can assess the significance of a variety of biological processes (Leigh *et al.*, 1993, 2004b; Nee, 2005; Gilbert *et al.*, 2006).

Why was neutral theory more popular among ecologists?

Finally, why the contrasting reception of neutral theory in population genetics vs. ecology? Population genetics was founded by evolutionary biologists (Fisher, 1918, 1930; Haldane, 1924, 1932; Wright, 1931, 1932). Darwin (1859) established the origin of adaptation as the central question of evolutionary biology, and population geneticists helped show how effectively natural selection shaped adaptation (Fisher, 1930; Haldane, 1932; Wright, 1932). Early on, Wright (1931:153) thought that differences between related species or genera were 'nonadaptive'. Gause's (1934) competitive exclusion principle, and careful studies such as that of Pittendrigh (1950) on how related species coexist, convinced most evolutionary biologists that most species differences were adaptive (Hutchinson, 1959; Mayr, 1963). Although Kimura never denied the importance of natural selection in adaptive evolution, many disliked his idea that most gene substitutions were neutral. Surely, as knowledge increased, the idea of neutral genes would melt away (Gillespie, 1991), as have the idea that species differences are nonadaptive, and the creationists' hope in unbridgeable missing links. Since 1930, Darwin's (1859, 1871) synthesis has acquired immense authority as the soundness of his judgment and the prescience of his vision have become progressively more evident. Nowadays, most 'anti-adaptationists' in evolutionary biology merely seek to replace a nearly automatic presumption of adaptation by shared standards for testing adaptive explanations (Orzack & Sober, 2001). In population genetics, no neutral theorist seeks to overthrow or marginalize adaptation by natural selection: here, the scope of the neutral theory controversy is comparatively limited.

Explaining genetic diversity triggered a bitter controversy that raged for many years. Was genetic diversity maintained by mutation–selection balance or by heterosis (Lewontin, 1974)? Balance between mutation and genetic drift presented a third possibility. Genetic diversity, however, increased far more slowly with population size than the neutral theory predicted (Lewontin, 1974:209). A 'nearly neutral' theory, based on a probability distribution of selective disadvantages of nearly neutral alleles, fit the relation between a population's size and its genetic diversity far better (Kimura, 1979), confirming the roles of both mutation–selection balance and neutral process in maintaining genetic diversity. The neutral theory reinforced the very fruitful (even if inexact) idea of clocked molecular phylogenies, continues to inspire elegant, creative mathematics (Ewens, 2004), provides useful null hypotheses (Donnelly & Tavaré, 1995; Kreitman & Akashi, 1995; Sabeti *et al.*, 2002), suggests the surprising importance of genetic drift in evolutionary change and accounts for patterns of nucleotide substitutions at silent sites (Ohta & Gillespie, 1996). Non-neutral population genetics, however, is still contributing significantly to evolutionary theory, not least by analyses of interactions between different levels of selection and other aspects of the evolution of cooperation (Maynard Smith & Szathmáry, 1995; see also Leigh & Rowell, 1995). Accordingly, few evolutionary biologists now view the neutral theory as the salvation of population genetics.

Unlike evolutionary theory, ecology lacks a founder who established a magisterial synthesis. Darwin (1859:110–116) sketched the outlines of an evolutionary ecology, implicitly based on a principle of competitive exclusion and explicitly based on his principle of 'divergence of character'. He also used island biology to outline an ecosystem ecology showing why larger land masses support more diversity and more intense competition, and are more resistant to introduced invaders (Darwin, 1859:104–108; Leigh *et al.*, 2007). Darwin's ideas, however, formed a few pages in his argument for the role of natural selection in evolution. Ecologists ignored them. Later, these ideas were rediscovered, in part, by Elton (1927), Lack (1947), Hutchinson (1959) and MacArthur (1961, 1972) among others. Many ecologists, however, denied the existence or the importance of density regulation and/or competitive exclusion (Andrewartha & Birch, 1954; Huston, 1994), even though these processes were central to Darwin's case for natural selection. The confusion was probably aggravated because theory played a less secure, less well-defined role in ecology than in evolution, where population genetics was based on Mendel's laws.

Ecologists divide sharply over what factors maintain species diversity, and why tropical settings are more diverse (Willig *et al.*, 2003; Leigh *et al.*, 2004b). Ecologists disagree on whether trade-offs and avoiding competitive exclusion are the keys to understanding species diversity (Huston, 1994; Leigh *et al.*, 2004b): no consensus is in sight. Some propose explicit mechanisms to explain diversity, such as the limitation of plant populations by specialized pests (Janzen, 1970), temporal segregation in recruitment (Chesson & Warner, 1981) and trade-offs such as growing fast in bright light vs. surviving in shade (Pacala *et al.*, 1996), or growing fast vs. investing in anti-herbivore defence (Fine *et al.*, 2006). Other explanations of diversity gradients, however, invoke factors such as mutation rate (Rohde, 1992) or aspects of climate (Hawkins *et al.*, 2003); here, the distinction between cause and correlation, and between causal processes and the environmental conditions that modulate their effects, is less clear. The neutral theory held out the hope of replacing a chaos of competing qualitative explanations of diversity that no argument, observation or experiment seemed able to resolve, by a theory capable of successful quantitative prediction. No wonder that some greeted the neutral theory as ecology's salvation.

There is a more fundamental issue. Everyone wants a quantitative theory that accounts for both pattern and the processes that generate it. No general theory in community ecology, however, has accomplished this. Neutral theorists have chosen to explain pattern, and ignore the processes that generate it: their critics prefer qualitative theory that deals with process. The contrasting attitudes to process of neutral theorists and their critics are illustrated by a neutral theorist's reaction to Leigh *et al.*'s (1993) demonstration that a set of four tree species is spreading nonrandomly quickly on 80-year-old islets without resident mammals in central Panama's Gatun Lake. Chave (2004:250) responded that 'only a few non-neutral species may have confused [this] analysis'. Where Chave saw confusion, Leigh *et al.* (1993) found a clue to why species diversity on these islets dropped nonrandomly quickly after they were isolated from the mainland. The four spreading species had large seeds, some of which escaped insect attack even if not buried, whereas seeds of most other large-seeded trees escape insect attack only if buried by agoutis. On these mammal-free islets, these four species have a great advantage over other large-seeded trees. The neutral theory could not explain the changes on these islets, but it provided the null hypothesis that helped to reveal what was happening there.

More generally, understanding a community's response to any kind of change requires knowledge of how species differ, and how these differences affect their responses to environmental change (Paine, 1974, 1992, 2002; Foster, 1990; Leigh *et al.*, 1993; King, 1994). Here, a qualitative theory of process is far more useful than a quantitative theory of pattern that cannot account for process.

This circumstance does not lack irony. Some decades ago, the ecological theory of competition-driven adaptive divergence drew its evidence from pattern, not process (see Hutchinson, 1959; MacArthur, 1960, 1969, 1972). This theory became focused on process and based on experiment (see, for example, Kitajima, 1994; Schluter, 1994; Fine *et al.*, 2004, 2006; Grant & Grant, 2006), largely thanks to prodding from critics such as Dayton (1973), Connor & Simberloff (1979) and Connell (1980). Thanks to their critics, proponents of adaptive divergence can now argue the importance of process to pattern-oriented neutral theorists.

The usefulness of the useless

A Chinese sage, Chuang Tzu, warned against ignoring the usefulness of the useless, remarking that 'only those who already know the value of the useless can be talked to about the useful' (Waley, 1939:3). His warning is especially apt for neutral theory. Neutral theory could rejuvenate forest ecology by uniting ecology and biogeography, especially if it includes evolution too. Its simple assumptions should enable neutral theory to base this synthesis on the limited dispersal of offspring from parents (Bramson *et al.*, 1996, 1998; Chave & Leigh, 2002), and predict:

1. species abundance distributions on different-sized plots, species–area curves over different scales and species turnover (the decreased similarity of species composition between two plots with increased distance between them) where extinction balances speciation and dispersal;
2. the manner, and the speed, of approach to the above equilibrium;
3. the changes, short and long term, of species composition on different-sized plots;
4. the distribution of different species' range sizes (Bell, 2001);
5. the rate of spread of new species lucky enough to survive; and
6. the average further lifetime of a species that now has N adults.

This synthesis should be supplemented by a submodel embodying a neutral theory of speciation. Hubbell (2001) foresaw many elements of this synthesis, but much of what he foresaw has yet to be done.

Such a synthesis would have many uses. First, it would serve as a model of what a more realistic theory should aim for. Second, there will be much to learn from why some neutral predictions are wrong. For example, understanding why the neutral theory of species–area curves fails for areas A in the range where the number S of species in area A varies as $S = cA^z$ might help us to decipher the biological basis of this empirical law.

Third, this synthesis will provide null hypotheses by which the effectiveness of different biological processes can be assessed (Nee, 2005). There is no point in disproving the neutral theory for the pleasure thereof: everyone, even its advocates, knows that its assumptions are wrong (Hubbell, 2001:6). Falsifying the neutral theory is useful only when its predictions are compared with those of other mechanistic hypotheses (McGill *et al.*, 2006:1421). A proper, spatially explicit, neutral theory would allow us to detect whether a species, or a collection of species, is spreading, or a plot's species composition changing, nonrandomly quickly (cf. Leigh *et al.*, 1993; Gilbert *et al.*, 2006). It might also enable us to decide whether the plant species growing together on a small plot, or those that have successfully colonized an oceanic island, are more distantly, or more closely, related than we would expect by chance. Does a plot's environment favour a set of related species (Webb, 2000), or do differences in physiological function or the specialized pests attracted allow plants to grow and survive better if their nearest neighbours are more distantly related (Cavender-Bares *et al.*, 2004; Webb *et al.*, 2006)?

Finally, neutral theory can serve as a stepping stone to a more realistic theory. Neutral theory may identify 'natural measures' of quantities, such as species diversity or similarity in species composition, which facilitate the development of more realistic theory (Leigh *et al.*, 2004a). Neutral theory provides methods for tackling more realistic problems. The variety of 'diffusion methods' in population genetics (Watterson, 1996) first used to study neutral processes (Fisher, 1922) has helped to solve a far wider range of problems (Kimura, 1994; Watterson, 1996; Ewens, 2004). Finally, Polya (1954) has emphasized the importance of solving related, simpler problems as stepping stones to solving more difficult ones. The neutral synthesis may often serve as this simpler stepping stone to developing a more realistic theory. For example, Zillio *et al.* (2005) modified neutral theory by assuming that each species was density regulated, as a first attempt at incorporating the effects of pest pressure. Neutral theory may serve as a particularly essential stepping stone to the spatially explicit theory ecology so sorely needs (Tilman & Kareiva, 1997). Often, the first neutral derivation will not permit generalization: only later ones will open practicable routes to a more realistic theory. The neutral theory will accordingly have little future unless some of its proponents revel in the beauty of its mathematics. An elegant, general, spatially explicit neutral theory, however, could provide an essential basis for both empirical and theoretical ecology.

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