

# Unified neutral theory of biodiversity and biogeography

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In response to a seemingly unresolvable plethora of explanations of how, especially in tropical settings, so many kinds of trees can coexist, Hubbell (1997, 2001) proposed neutral theory to explain biodiversity patterns without invoking species differences. Neutral theory assumes that each individual's prospects of death and reproduction are independent of what species it, or its neighbors, belong to (Hubbell 2001). This assumption is simple enough to allow neutral theory to unify diverse aspects of ecology and biogeography such as species abundance distributions, changes in species composition over space and time, and the impacts of habitat fragmentation in a “**unified neutral theory of biodiversity and biogeography**” (Hubbell, 2001). Hubbell's theory is modeled on neutral theory in population genetics, where within a species, each individual's prospects of death and reproduction are independent of its genotype (Kimura, 1983). Ecologists apply neutral theory within a single trophic level, usually trees, sometimes corals or other guilds (Hubbell, 1997, 2001).



Figure 1: A tropical rainforest (Mt. Kinabalu, Malaysian Borneo) photographer: James Rosindell

## Uses of neutral theory

Neutral theory focuses on the numbers of species in different-sized areas, their relative abundance, and how species composition changes from time to time and from place to place. Like its population genetics counterpart, ecological neutral theory serves as a null hypothesis, generates mathematical techniques useful for more realistic theory, provides some tractable first approximations to reality, identifies factors crucial to understanding various questions, and brings many topics within a common perspective.

## Species abundance distributions

## Historical perspective

Neutral theory was initially welcomed because it offered a simple mechanistic explanation of species abundance distributions (Caswell, 1976; Hubbell, 1979, 1997; Bell, 2000, 2001). Moreover, neutral theory's lack of processes stabilizing species abundances allowed it to represent diversity as a balance between speciation and extinction (Hubbell, 2001). At first, computer simulations were used to explore the range of species abundance distributions neutral theory might explain (Hubbell, 1979, 1997, 2001; Bell, 2000, 2001): despite differences in how community size was regulated, Bell's and Hubbell's results were similar. Matching the species abundance distributions of trees  $\geq 10$  cm dbh on 50-ha forest plots by analytically derived neutral formulae (Etienne and Olff, 2005) was considered neutral theory's greatest triumph (Hubbell, 2006). Many were attracted by a theory with no mechanisms to stabilize species abundances.

## The basic framework

In the best-known neutral model, at each time-step one adult is appointed at random from the community to die, and another to produce the immediately maturing replacement young. With probability  $u$  this young founds a new species. This model employs the formalism of a population genetics model for a locus with many equally fit alleles in a population of  $N$  haploid reproductives. Genes at this locus now represent individuals, alleles represent species, and mutation represents speciation. Genes reproduce uniparentally; therefore, ecological neutral theory's individuals must also. They can be parthenogenetic, or hermaphrodites capable of selfing, where the mother counts as the parent, or one can count only females.

## Calculating the simplest species-abundance distribution

Neutral theory seeks precise, testable predictions from simple assumptions. To illustrate the power of its assumptions, we derive a species abundance distribution, the number  $\varphi(j)$  of species with  $j$  reproductive adults apiece in a community with  $N$  adults in all. To do this, we assume

- 1. This distribution  $\varphi(j)$  does not change with time: it is in a steady state where speciation balances random extinction.
- 2.  $N$  is constant. This is the "zero-sum" assumption, which can be relaxed with little change (Etienne et al., 2007; Haegeman and Etienne, 2008).
- 3. Each individual has probability  $u$  of being an entirely new species. This assumption can also be relaxed (Rosindell et al., 2010).
- 4. The population is panmictic: each adult has equal chance of mating with any other, including itself. Many neutral theorists have tried to circumvent this assumption (Bramson et al., 1996, 1998; Economo and Keitt, 2008; Rosindell and Cornell, 2009).
- 5. At each time-step, one of these  $N$  adults, chosen at random, dies, and another produces the immediately maturing replacement young. Caswell (1976) and Leigh (2007) let the newly dead be an eligible parent of its replacement, whereas Hubbell (1979) and Etienne and Olff (2004) chose this parent from the  $N - 1$  survivors. We follow Caswell's convention: Hubbell's yields similar results (Etienne and Alonso, 2007).

The fifth assumption embodies the fundamental neutral premise that each individual's prospects of death or reproduction are independent of its species: the others are merely "carrier assumptions" which simplify the mathematics.

We now calculate the species abundance distribution implied by these assumptions. At a given time-step the probability  $P(1, 0)$  that the one surviving member of a species dies and either does not reproduce, or, with probability  $u$ , bears a young of a new species, is  $\frac{1}{N} \frac{(N-1+u)}{N} \approx \frac{(N-1)}{N^2}$ , whereas the probability that its replacement will be a new species,  $P(0, 1)$  is  $u$ . At steady state, origin balances extinction, so  $\varphi(1)P(1, 0) = \varphi(1) \frac{(N-1)}{N^2} = P(0, 1) = u$ , and  $\varphi(1) = u \frac{N^2}{N-1}$ . The probability  $P(j, j-1)$  that a member of a species with  $j$  adults dies at this time-step and is replaced by another species is nearly  $\frac{j(N-j)}{N^2}$ ; the probability  $P(j-1, j)$  that one of a species's  $j-1$  members bears a conspecific young replacing another species's dead is  $\frac{(j-1)(N-j+1)(1-u)}{N^2}$ . At steady state,  $\varphi(j-1)P(j-1, j) = \varphi(j)P(j, j-1)$ ,  $1 < j \leq N$ . If  $j \ll N$ , then  $\varphi(j)$  is nearly

$$\frac{uN^2(1-u)^{j-1}}{j(N-j)} = \frac{N\theta(1-u)^j}{j(N-j)} \approx \frac{\theta x^j}{j}$$

Here,  $\theta$ , Hubbell's fundamental biodiversity number, is  $\frac{uN}{(1-u)}$ , and  $x = 1 - u$ . When species diversity is high (Alonso & McKane, 2004), this distribution approximates Fisher et al.'s (1943) log series  $\varphi(j) = \frac{1}{j} \alpha x^j$ , where Fisher's  $\alpha = \theta$ . This distribution does not depend on the details of life-history. If each generations has  $N$  adults apiece, which result from sampling the previous generation's adults  $N$  times with replacement, each parent contributing as many young to the next generation as the times it was sampled, the distribution is the same,  $\varphi(j) \approx \frac{1}{j} \theta x^j$ , but  $\theta = 2Nu$  (Hubbell, 2001; Etienne and Alonso, 2007). If each living adult has identical prospects of growth, and if its probability of death (but not of reproduction!) is proportional to its size, the species abundance distribution is unchanged (O'Dwyer et al., 2009b).

### Plots receiving migrants from panmictic source pools

Seeds disperse only limited distances from their parents. Hubbell (1997, 2001), Vallade and Houchmandzadeh (2003, 2006), Etienne and Olff (2004), and Etienne and Alonso (2007) incorporated this departure from panmixia by considering a forest plot small enough to be panmictic ( $< 5 \text{ km}^2$ : Zillio and Condit 2007), where speciation is negligible. When a tree on the plot dies, with probability  $m$  its replacement's parent is chosen from a large, panmictic source pool, where speciation balances random extinction; with probability  $1 - m$  this parent is chosen from the plot. This model is called "spatially implicit" (Hubbell, 2001). Volkov et al. (2003) provide a simple derivation of such plots' species abundance distributions. The contrast between source pool and plot parallels the ecological distinction between regional diversity, where speciation balances extinction, and local diversity, where immigration balances local extinction (Leigh et al. 2004), a distinction foreshadowed by MacArthur and Wilson (1967)'s distinction between a continental source and offshore islands. Ecological neutral theorists often refer to the source pool as a metacommunity, but metacommunities usually imply systems of semi-isolated patches, whereas no one has yet avoided

assuming a panmictic source community. The spatially implicit neutral model predicts fewer rare species than the log series. To fit species-abundance distributions to empirical data, one employs an easily-used formula of Etienne (2005), too complicated to derive or present here, to choose parameters that optimize the probability of observing the sampled data given the model.

## Evaluating neutral explanations of species-abundance distributions

Evaluating neutral explanations of species-abundance distributions has presented several problems. Resolving these problems has been important, not only for species abundance distributions, but for neutral theory as a whole.

### Interpreting the speciation parameter

How could one believe, as traditional neutral theory (Hubbell, 2001) asserts, that each species arises from one parthenogenetic individual (Ricklefs, 2003)? Hubbell (2001) modeled speciation as random splitting of ancestral populations, but doing so fits the data far less well than Hubbell's original model (Etienne and Haegeman, 2010). To start each new species with several members, not just one, and to incorporate the idea that speciation is a process that takes time, Rosindell et al. (2010) developed a model of "protracted speciation" where each individual has probability  $u$  of being a new "variant," as yet undetectable. If this variant has any descendants  $\tau$  generations later, they become a new species, in which case it starts with an average of  $\tau + 1$  members. If  $\tau \ll N$ , starting new species this way does not affect the observable parts of the species-abundance distribution, but it changes neutral theory predictions about phylogenies, diminishes the speciation rate needed to fit the distribution, and increases mean species lifetime to a more reasonable level.

$Nu$  now becomes the number of individuals of new species entering the community each generation. Other evidence suggests that most species begin as fairly small populations (Leigh et al., 2004). To calculate the average initial number of adults per new species in Rosindell's model, use the generating function (Fisher, 1930)

$$f_{\tau}(s) = \sum_{k=0}^{\infty} p_k(\tau) s^k$$

where the coefficient of  $s^k$  is the probability that the variant has  $k$  descendants  $\tau$  generations later.

Generating functions incarnate the ideas that each individual has the same prospects of death or reproduction, while the fate of each is independent of all others. We start with one variant:

$f_0(s) = s$ . As different individuals reproduce independently,  $f_{\tau+w}(s) = f_{\tau}[f_w(s)]$ . Let an individual alive at time  $\tau$  have probability  $d\tau$  of dying, and independent probability  $d\tau$  of reproducing, by time  $\tau + d\tau$ . Then

$$f_{d\tau}(s) \approx d\tau + (1 - 2d\tau)s + d\tau s^2 = s + (1 - s)^2 d\tau$$

$$f_{d\tau}[f_{\tau}(s)] = f_{\tau+d\tau}(s) = f_{\tau}(s) + [1 - f_{\tau}(s)]^2 d\tau$$

$$f_{\tau+d\tau}(s) - f_{\tau}(s) = df_{\tau}(s) = [1 - f_{\tau}(s)]^2 d\tau$$

$$d\tau = \frac{df_{\tau}(s)}{[1 - f_{\tau}(s)]^2}$$

$$f_{\tau}(s) = \frac{[\tau + s(1 - \tau)]}{(1 + \tau - s\tau)}$$

The probability of no descendants at time  $\tau$  is  $f_{\tau}(0) = \frac{\tau}{1 + \tau}$ . As the expected number of descendants at each generation is 1, the expected number of descendants  $\tau$  generations later, if the lineage still survives, is  $\tau + 1$ , and the probability that an individual is born into a species new that generation is  $u$ .

## Dynamics and species-abundance distributions

Many processes lead to the same species-abundance distribution (Bell, 2000; McGill et al., 2006, 2009), yet neutralists rarely test the dynamics from which their species-abundance distributions are derived. On one well-fit 50-ha plot, in Barro Colorado Island, Panama, deaths and recruitments of most of the 20 commonest tree species are in significant imbalance, confirming that a well-fit species-abundance distribution does not imply neutral dynamics (Leigh 2007). Moreover, very common species die out much more quickly than neutral theory predicts: after all, the expected lifetime of a neutral population with  $N$  reproductives is  $N$  generations (Leigh, 1981; Ricklefs, 2006). Ironically, although neutral theory's lack of stabilizing mechanisms allows successive replacement of species in time (Hubbell, 2009), in nature species replace each other much more quickly than neutral theory predicts: some non-neutral process, such as environmental change, must cause these extinctions (Leigh, 1981).

## Testing the predictive value of neutral species-abundance distributions

Woodcock et al. (2007) tested the predictive value of the neutral model of species abundance distributions in "plots" of different sizes receiving migrants at the same rate  $m$  from the same source pool. Their "plots" were 29 tree holes in a 10 km<sup>2</sup> tract of beech forest, with water contents between 50 and 18,000 ml. They drained each hole, estimated its bacterial population, homogenized the drained water, and sampled 500,000 bacteria from it. They calculated  $m$  and source pool  $\theta$  from the distribution of abundance of the more common species in the sample from the smallest tree hole, and predicted this distribution for other holes with different numbers of bacteria, a much stronger test than fitting the species abundance distribution to a single plot. Their predictions were remarkably accurate. We know little of bacterial dynamics in nature, but this test suggests that these tree holes are receiving their bacteria from the same source pool.

## Independently estimating parameters of species-abundance distributions

Neutralists rarely provide independent estimates of fitted parameters such as the fundamental biodiversity number  $\theta = \frac{Nu}{1 - u}$  or the rate  $m$  of immigration into the plot from the source pool (McGill et al. 2006). Indeed, McGill et al. find that the estimate of  $\theta$  depends on sample size. Moreover, no sound way has yet been found to measure  $N$  and  $u$  independently. On some plots, the more direct measures of immigration rate  $m$  of Leigh et al., (2004b: 260-261) and Chisholm and Lichstein (2009) differ greatly from the estimates provided by Etienne's sampling formula (Leigh, 2007). Only recently have neutral theorists begun to question the notion of a panmictic source pool (Etienne, 2007) and to develop spatially explicit models instead. Chave et al. (2002) have simulated species-abundance distributions on a spatially explicit basis. Only Bramson et al. (1998) have tried to

derive species abundance distributions where seeds disperse limited distances from their parents.

### More tools for testing ecological neutral theory

An easily measured parameter, put to good use by Malécot (1949), is the probability  $F(t)$  that two individuals randomly sampled from the community of  $N$  at time  $t$  are the same species. Then

$$F\left(t + \frac{1}{N}\right) = \left(1 - \frac{2}{N}\right) F(t) + \left(\frac{2}{N}\right) \left[\frac{1}{N} + \left(1 - \frac{1}{N}\right) F(t)\right] (1 - u)$$

Here, with probability  $1 - \frac{2}{N}$ , neither of our pair dies at the next time-step, so  $F$  does not change.

With probability  $\frac{2}{N}$ , one does die. If so, with probability  $\frac{1 - u}{N}$ , its replacement is the unmutated young of the survivor; with probability  $\left(1 - \frac{1}{N}\right) (1 - u) F(t)$  its replacement is the unmutated young of some other conspecific. At steady state,

$$F\left(t + \frac{1}{N}\right) = F(t) = F = \frac{1 - u}{1 - u + uN} = \frac{1}{1 + \frac{uN}{1 - u}} = \frac{1}{1 + \theta}$$

Finding  $\theta$  from the equation  $S = \theta \ln\left(1 + \frac{N}{\theta}\right)$  (Fisher et al., 1943: 55), where  $S$  is the community's number of species, a distribution's fit to the log series is reflected by the relation

$$F = \frac{1}{1 + \theta}.$$

Now let a plot exchange migrants with a large source pool whose  $F$  is  $F^*$ .  $F^*$  is also the probability that a migrant from the source pool is conspecific with a random individual in the plot. Then, in strict analogy with the previous equation, the plot's  $F$  is

$$F = \left(1 - \frac{2}{N}\right) F + \frac{2}{N} \left[ mF^* + (1 - m) \left(\frac{1}{N} + \left(1 - \frac{1}{N}\right) F\right) \right]$$

Let  $H$ , the probability  $1 - F$  that two sampled individuals belong to different species, measure

diversity. Set  $I = \frac{mN}{1 - m}$ . Then, if the source pool follows a log series with  $1 - F^* = \frac{\theta}{1 + \theta}$ ,

$\frac{1 - F}{1 - F^*} = \frac{I}{I + 1}$  (Etienne, 2005). In 1995,  $F$  was  $\frac{1}{38}$  for the 21455 trees  $\geq 10$  cm dbh on the 50-ha plot in Barro Colorado Island, Panama (Leigh, 2007), while Hubbell's (2001) estimate of source pool  $\theta$ , based on the plot's more common trees, was 50, implying that  $F^* = \frac{1}{51}$ . Here, Etienne's (2005)

relationship implies that  $m = 0.0067$ , a striking contrast with the  $m = 0.093$  calculated from Etienne's sampling formula. We do not fully understand this discrepancy.

## Moving beyond species abundance distributions

### Neutral theory and fragmentation

Let a new reservoir create completely isolated islands, which receive no migrants. How fast does an

island's tree diversity decline? How quickly do its rare species disappear? How fast does its species composition change? How does similarity of species composition between pairs of islands change? First, measure an island's tree diversity by  $H(t) = 1 - F(t)$ , where  $F(t)$  is the probability that two of its  $N$  trees, sampled at random with replacement at time  $t$ , are the same species. Each time-step, a tree dies: measure time in generations of  $N$  time-steps apiece. Setting  $u = 0$  in the basic equation for  $H = 1 - F$ , we find (Leigh, 2007),

$$H(t + \frac{1}{N}) = H(t) \left[ 1 - \left(\frac{2}{N}\right) \left(1 - \frac{1}{N}\right) H(t) \right], \quad \frac{dH}{dt} \approx \frac{-2H(t)}{N}$$

Next, what is the probability that a species with  $k$  trees on this island at time 0,  $k \ll N$ , disappears by generation  $t$ ? If the species has one tree at time 0, the probability that the species disappears from the island by generation  $t$  is  $\frac{t}{1+t}$ , as we showed when discussing "protracted speciation". As disappearance of descendants of different trees are nearly independent events, the probability that a species with  $j \ll N$  trees at  $t = 0$  disappears from the island by time  $t$  is roughly  $\left(\frac{t}{1+t}\right)^j$ . Now consider how a newly isolated island's species composition should change. If a species has  $j$  trees on the island at time 0, the probability is  $\frac{j}{N}$  that one dies, and  $\frac{j}{N}$  that one reproduces by time  $\frac{1}{N}$ . Thus, by time  $t$ , this species will suffer an average of  $2jt$  births and deaths (Gilbert et al., 2006). As births and deaths are equally likely, the mean square population change, the mean square of the number of births less the number of deaths, is  $2jt$ , the mean square difference between the number of heads and the number of tails in  $2jt$  tosses of a fair coin. Because the plot has  $N$  trees, the expected sum of the squared population changes of all species on the plot is roughly  $2Nt$  if  $t \ll N$  (Gilbert et al., 2006). The distribution of this sum about its mean has yet to be derived. Let  $F_{jk}(t)$  be the probability that two trees sampled at random at time  $t$ , one from island  $j$ , one from island  $k$ , are the same species. As species composition changes independently on the two islands (they exchange no migrants, and there is no selection), the expected value of  $F_{jk}(t)$  does not change. Eventually, the chances of death and reproduction leave only one species on each island: the probability that the same species takes over both islands is  $F_{jk}(t)$ . How the distribution of  $F_{jk}(t + s)$  changes as  $s$  increases, for given value of  $F_{jk}(t)$ , is not yet known. For islets < 1 ha isolated by Panama's Gatun Lake after the Chagres was dammed in 1910, all three predictions were tested. Tree diversity on small islands declined more rapidly, and species composition changed more quickly, than neutral theory predicts. Finally, a set of four large-seeded tree species, whose seeds did not need burial by agoutis to escape insect attack, were taking over these islands (Leigh et al. 1993).

### Neutral theory and species turnover

Spatially explicit models can predict species turnover and species-area curves. Following Nagylaki (1974) in population genetics, Chave and Leigh (2002) modeled species turnover in a uniform forest of infinite extent. When a tree died, a distance was sampled from the probability distribution  $P(r)$  of a tree being  $> r$  m from its seed-parent, and a direction chosen at random. The tree nearest the point the sampled distance and direction from the dead tree became the seed-parent of its immediately maturing replacement. When  $P(r)$  is the bivariate Gaussian  $\exp\left(\frac{-r^2}{\sigma^2}\right)$ , where  $\sigma^2$  is the mean square dispersal distance of young from seed-parent, these assumptions suffice to derive the probability  $F(r)$  that, at steady state where speciation balances random extinction, two trees  $r$  km

apart are the same species, as a function of  $\sigma^2$ , tree density, and speciation rate  $u$ . This theory's  $F(r)$  fit trends in the data for lowland forest in southwestern Peru, Amazonian Ecuador and central Panama. Speciation rates fitting these data differ wildly:  $4.8 \times 10^{-8}$  in Panama and  $1.7 \times 10^{-14}$  in Peru (Condit et al., 2002). Nonetheless, this model focused attention on tree species turnover, showed that turnover arises because species originate in different places and spread limited distances (Sawyer and Fleischman, 1979) and provided a useful null hypothesis of species turnover.

## Neutral theory and species-area curves

Species-area curves are often used in ecological research (MacArthur and Wilson, 1967: 8-18; Rosenzweig, 1995). The number of species  $S$  in an area  $A$  is usually proportional to  $A^z$ , with most  $z$  between 0.2 and 0.35 (MacArthur and Wilson, 1967:17). Durrett and Levin (1996) first simulated species-area curves based on neutral dynamics: they assumed that an individual's young could disperse no further than a site occupied by a nearest neighbor. Chave et al. (2002) simulated species-area curves assuming a far wider range of possible dispersal distances. Most of these simulations, however, assumed communities of no more than a million individuals. Bramson et al. (1996) analytically calculated species-area curves based on neutral dynamics and nearest-neighbor dispersal, but these curves did not match empirical counterparts. More recently, Rosindell and Cornell (2009) simulated species-area curves  $S(A)$  for plots of area  $A$  within an infinite landscape as a function of speciation rate, tree density, and distribution of distances from seed-parent to young. Setting the probability  $P(r)$  that a tree is  $> r$  m from its seed-parent equal to  $\exp\left(\frac{-r^2}{\sigma^2}\right)$  yielded

unrealistic species-area curves. Setting  $P(r) = \left(1 + \frac{r^2}{L^2}\right)^{-k}$ ,  $k \leq 2.0$ , yielded realistic curves

where, over a wide range of areas  $A$ ,  $S(A) \approx cA^z$ , where  $c$  is a constant (Rosindell and Cornell, 2009). This circumstance confirms observations that natural distributions of parent-offspring distances are normally fat-tailed (Clark et al., 1999). O'Dwyer and Green (2009) unified the spatially explicit theories of species-area curves and species turnover, assuming a radially symmetric exponential distribution of distances from seed-parent to seed, and derived an explicit formula for species-area curves. Their prediction for the probability  $F(r)$  that two trees a distance  $r$  apart are conspecific approximates but does not quite match Chave and Leigh (2002)'s exact calculation. One notable finding is that, for the range of areas for which  $S(A) \approx cA^z$ ,

$$z = \frac{4 \left[ \ln\left(\frac{1}{u}\right) + \ln \ln\left(\frac{1}{u}\right) \right]}{\ln\left(\frac{1}{u}\right) \left[ \ln\left(\frac{1}{u}\right) + 2 \ln \ln\left(\frac{1}{u}\right) \right]}$$

This equation relates speciation rate  $u$  to the observable  $z$ . Can their approach fulfill neutral theorists' ambition for a unified neutral theory of biodiversity and biogeography? To do so, it must assume fat-tailed distributions of dispersal distances, which may prove difficult.

## Impacts of ecological neutral theory

### Neutral theory: a teething ring for theoreticians

Neutral theory provides springboards for tackling more complex problems, such as deriving the species-abundance distribution when each species is subject to the same intensity of intra-specific



density dependence. Consider, for example, a source pool with  $N$  individuals where at each time-step the probabilities of a death, or a birth to a conspecific, in a species with  $j$  individuals, are  $\frac{jd_j}{N} = \frac{j}{N}$  and  $\frac{jb_j}{N} = \frac{j(1-u)}{N}$  respectively. The number of species with  $j$  individuals apiece,  $\varphi(j)$ , is therefore

$$Nu \prod_{i=1}^{j-1} \frac{ib_i}{(i+1)d_{i+1}} = Nu \prod_{i=1}^{j-1} \frac{i(1-u)}{i+1} = \frac{Nu(1-u)^j}{(1-u)^j}$$

Volkov et al. (2005) let the birth and death rates of each species in the source pool vary with its density in the same way. They set  $b_i = b \left(1 + \frac{p}{i}\right)$  and  $d_i = d \left(1 + \frac{q}{i}\right)$ , where  $bp > dq$  (Azaele et al., 2006), so that the average change in the species's population per time-step is  $\frac{bp - dq + (b-d)i}{N}$ .

This is an unrealistic equation for a population's dynamics. There is no reason, however, why density dependence cannot be modeled more realistically (cf. Leigh, 1975: 67-68). Doubtless, neutral theory will develop many more mathematical techniques that will bear fruit in other contexts, as population genetics has done before.

### Neutral theory as a null hypothesis

Ecological neutral theory, like its population genetics counterpart, has been most useful as a null hypothesis. For example, neutral theory predicts that if a single adult, or a group of  $n$  adults, has descendants  $t$  generations later, with probability nearly  $\exp(-k)$  they will have  $> kt$  descendants then if  $n \ll t$  (Leigh, 2007). Trees of the genus *Ocotea* dispersed across the sea from North to South America 20,000,000 years ago,  $< 1,000,000$  tree generations ago. This genus has since spread throughout tropical America, which must have had  $> 20,000,000$  *Ocotea* reproductives even during Pleistocene droughts. Testing the null hypothesis that *Ocotea* was a neutral clade invading a neutral community showed that *Ocotea* differed in ways that allowed it to reproduce significantly faster than the natives. According to neutral theory, this advantage should have let it take over the forest (Zhang & Lin, 1997), but it did not. Therefore, the invading *Ocotea* must have differed from the forest's other species in ways that allowed it to coexist with them. Ergo, fully understanding tropical tree diversity involves learning how differences among tree species allow them to coexist, a conclusion that was far from obvious before the advent of neutral theory.

### Neutral theory and biological reality

Despite its simple assumptions, neutral theory sometimes points toward truth. It suggested that most tree species begin as fairly small populations, and that in most tree species, the distribution of dispersal distances from seed-parent to seed is "fat-tailed." Considering plots receiving migrants from large source pools proved enormously stimulating. How low immigration — or limited seed production — affects a plot's species composition raised the question, how selective of microsites can a plant species be? How likely are its seeds to land in suitable places? More generally, does a plot's species composition reflect what seeds happened to get there (dispersal assembly), or what species grow best there (niche assembly)? Neutral theory also focuses attention on inadequately studied questions such as species turnover. Finally, by setting various topics in a wider perspective, neutral theory raises hopes for achieving a more general, widely-ranging theory of species diversity.

## References

- Alonso, D. & A. J. McKane. 2004. Sampling Hubbell's neutral model of biodiversity. *Ecology Letters* 7: 901-910.
- Azaele, S., S. Pigolotti, J. R. Banavar & A. Maritan. 2006. Dynamical evolution of ecosystems. *Nature* 444: 926-928.
- Bell, G. 2000. The distribution of abundance in neutral communities. *American Naturalist* 155: 606-617.
- Bell, G. 2001. Neutral macroecology. *Science* 293: 2413-2418.
- Bramson, M., J. T. Cox & R. Durrett. 1996. Spatial models for species-area curves. *Annals of Probability* 24: 1727-1751.
- Bramson, M., J. T. Cox & R. Durrett. 1998. A spatial model for the abundance of species. *Annals of Probability* 28: 658-709.
- Caswell, H. 1976. Community structure: a neutral model analysis. *Ecological Monographs* 46: 327-354.
- Chave, J. & E. G. Leigh, Jr. 2002. A spatially explicit neutral model of  $\beta$ -diversity in tropical forests. *Theoretical Population Biology* 62: 153-168.
- Chave, J., H. C. Muller-Landau & S. A. Levin. 2002. Comparing classical community models: Theoretical consequences for patterns of diversity. *American Naturalist* 159: 1-23.
- Chisholm, R. A. & Lichstein, J. W. 2009. Linking dispersal, immigration and scale in the neutral theory of biodiversity. *Ecology Letters* 12: 1385-1393.
- Clark, J. S., M. Silman, R. Kern, E. Macklin & J. HilleRisLambers. 1999. Seed dispersal near and far: patterns among temperate and tropical forests. *Ecology* 80: 1475-1494.
- Condit, R., N. Pitman, E. G. Leigh, Jr., J. Chave, J. Terborgh, R. B. Foster, P. Núñez V., S. Aguilar, R. Valencia, G. Villa, H. C. Muller-Landau, E. Losos & S. P. Hubbell. 2002. Beta-diversity in tropical forest trees. *Science* 295: 666-669.
- Durrett, R. & S. Levin. 1996. Spatial models for species-area curves. *Journal of Theoretical Biology* 179: 119-127.
- Economo, E. P. & T. H. Keitt. 2008. Species diversity in neutral metacommunities: a network approach. *Ecology Letters* 11: 52-62.
- Etienne, R. S. 2007. A neutral sampling formula for multiple samples and an 'exact' test of neutrality. *Ecology Letters* 10: 608-618.
- Etienne, R. S. & D. Alonso. 2007. Neutral community theory: how stochasticity and dispersal-limitation can explain species coexistence. *Journal of Statistical Physics* 128: 485-510.
- Etienne, R. S., D. Alonso & A. J. McKane. 2007. The zero-sum assumption in neutral

biodiversity theory. *Journal of Theoretical Biology* 248: 522-536.

- Etienne, R. S. & B. Haegeman. 2010. The neutral theory of biodiversity with random fission speciation. *Theoretical Ecology*. DOI 10.1007/s12080-010-0076-y
- Etienne, R. S. & H. Olf. 2004. A novel genealogical approach to neutral biodiversity theory. *Ecology Letters* 7: 170-175.
- Etienne, R. S. & H. Olf. 2005. Bayesian analysis of species-abundance data : assessing the relative importance of dispersal and niche-partitioning for the maintenance of diversity. *Ecology Letters* 8: 493-504.
- Fisher, R. A. 1930. *The Genetical Theory of Natural Selection*. Clarendon Press, Oxford.
- Fisher, R. A., A. S. Corbet & 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.
- Gilbert, B., W. F. Laurance, E. G. Leigh, Jr. & H. E. M. Nascimento. 2006. Can neutral theory predict the responses of Amazonian tree communities to forest fragmentation? *American Naturalist* 168: 304-317.
- Haegeman, B. & R. S. Etienne. 2008. Relaxing the zero-sum assumption in neutral biodiversity theory. *Journal of Theoretical Biology* 252 : 288-294.
- Hubbell, S. P. 1979. Tree dispersion, abundance and diversity in a tropical dry forest. *Science* 203: 1299-1309.
- Hubbell, S. P. 1997. A unified neutral theory of biogeography and relative species abundance and its application to tropical rain forests and coral reefs. *Coral Reefs* 16, suppl. S9-S21.
- Hubbell, S. P. 2001. *The Unified Neutral Theory of Biodiversity and Biogeography*. Princeton University Press, Princeton, N. J.
- Hubbell, S. P. 2009. Neutral theory and the theory of island biogeography. Pp. 264-292 in J. Losos & R. E. Ricklefs, eds. *The Theory of Island Biogeography Revisited*. Princeton University Press, Princeton, NJ.
- Kimura, M. 1983. *The Neutral Theory of Molecular Evolution*. Cambridge University Press, Cambridge.
- Leigh, E. G., Jr. 1975. Population fluctuations, community stability, and environmental variability. Pp. 51-73 in M. L. Cody & J. M. Diamond, eds. *Ecology and Evolution of Communities*. Harvard University Press, Cambridge, MA.
- Leigh, E. G. Jr. 1981. The average lifetime of a population in a varying environment. *Journal of Theoretical Biology* 90: 213-239.
- Leigh, E. G., Jr. 2007. Neutral theory: a historical perspective. *Journal of Evolutionary Biology* 20: 2075-2091.
- Leigh, E. G., Jr., P. Davidar, C. W. Dick, J.-P. Puyravaud, J. Terborgh, H. ter Steege & S. J.

Wright. 2004. Why do some tropical forests have so many species of trees? *Biotropica* 36: 447-473.

- Leigh, E. G., Jr., R. Condit & S. Loo de Lao. 2004b. The neutral theory of forest ecology. Pp. 244-263 in E. C. Losos & E. G. Leigh, Jr., eds. *Tropical Forest Diversity and Dynamism*. University of Chicago Press, Chicago, IL.
- Leigh, E. G., Jr., S. J. Wright, F. E. Putz & 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.
- MacArthur, R. H. & E. O. Wilson. 1967. *The Theory of Island Biogeography*. Princeton University Press, Princeton, NJ.
- McGill, B. J., R. S. Etienne, J. S. Gray, D. Alonso, M. J. Anderson et al. 2007. Species abundance distributions : moving beyond single prediction theories to integration within an ecological framework. *Ecology Letters* 10: 995-1015.
- McGill, B. J., B. A. Maurer & M. D. Weiser. 2006. Empirical evaluation of neutral theory. *Ecology* 87: 1411-1423.
- Malécot, G. 1949. *Les Mathématiques de la Hérité*. Masson et Cie., Paris.
- Nagylaki, T. 1974. The decay of genetic variability in geographically structured populations. *Proceedings of the National Academy of Sciences, USA* 71: 2932-2936.
- O'Dwyer, J. P. and J. L. Green. 2009. Field theory for biogeography: a spatially explicit model for predicting patterns of biodiversity. *Ecology Letters* 12: 1-9.
- O'Dwyer, J. P., J. K. Lake, A. Ostling, V. M. Savage & J. L. Green. 2009b. An integrative framework for stochastic size-structured, community assembly. *Proceedings of the National Academy of Sciences* 106: 6170-6175.
- Ricklefs, R. E. 2003. A comment on Hubbell's zero-sum ecological drift model. *Oikos* 100: 185-192.
- Ricklefs, R. E. 2006. The unified neutral theory of biodiversity: Do the numbers add up? *Ecology* 87: 1424-1431.
- Rosenzweig, M. L. 1995. *Species Diversity in Space and Time*. Cambridge University Press, Cambridge.
- Rosindell, J. & S. J. Cornell. 2009. Species-area curves, neutral models, and long-distance dispersal. *Ecology* 90: 1743-1750.
- Rosindell, J., S. J. Cornell, S. P. Hubbell and R. S. Etienne. 2010. Protracted speciation revitalizes the neutral theory of biodiversity. *Ecology Letters* 13: 716-727.
- Sawyer, S. & J. Fleischman. 1979. Maximum geographic range of a mutant allele considered as a subtype of a Brownian branching random field. *Proceedings of the National Academy of Sciences, USA* 76: 872-875.

- Vallade, M. & B. Houchmandzadeh. 2003. Analytical solution of a neutral model of biodiversity. *Physical Review E* 68, 061902.
- Vallade, M. & B. Houchmandzadeh. 2006. Species abundance distribution and population dynamics in a two-community model of neutral ecology. *Physical Review E* 74, 051914.
- Volkov, I., J. R. Banavar, F. He, S. P. Hubbell & A. Maritan. 2005. Density dependence explains tree species abundance and diversity in tropical forests. *Nature* 438: 658-661.
- Volkov, I., J. R. Banavar, S. P. Hubbell & A. Maritan. 2003. Neutral theory and relative species abundance in ecology. *Nature* 424: 1035-1037.
- Woodcock, S., C. J. van der Gast, T. Bell, M. Lunn, T. P. Curtis, I. M. Head & W. T. Sloan. 2007. Neutral assembly of bacterial communities. *FEMS Microbial Ecology* 62: 171-180.
- Zhang, D.-Y. & K. Lin. 1997. The effects of competitive asymmetry on the rate of competitive displacement: how robust is Hubbell's community drift model? *Journal of Theoretical Biology* 188: 361-367.
- Zillio, T. & R. Condit. 2007. The impact of neutrality, niche differentiation and species input on diversity and abundance distributions. *Oikos* 116: 931-940.

## External links

- Publisher of 'The Unified Neutral Theory of Biodiversity and Biogeography' (<http://press.princeton.edu/chapters/s7105.html>)
- Wikipedia page on neutral theory ([http://en.wikipedia.org/wiki/Unified\\_neutral\\_theory\\_of\\_biodiversity](http://en.wikipedia.org/wiki/Unified_neutral_theory_of_biodiversity))

## See also

- Speciation, Biodiversity

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