

Neutrality, Niche, and Nulls: Causal Relevance in Ecology¹

Jay Odenbaugh
Department of Philosophy
Lewis and Clark College
jay@lclark.edu

Key words: abstraction, biodiversity, biogeography, causal relevance, difference-making, ecology, idealization, neutral, niche, null hypothesis, model, realism, robustness

I. Introduction. In 2001, ecologists found themselves genuinely befuddled. Stephen Hubbell had published his book *The Unified Neutral Theory of Biodiversity and Biogeography* in which provided a “neutral” model of community and landscape ecological phenomena that was extremely accurate in its predictions. The befuddlement arose because of the neutrality assumption; namely, all of the individuals in a given trophic level in a community are “ecologically equivalent.” That is, individuals are *exactly the same* in their ecological properties such as the probability of giving birth and dying. Ecologists of course know this is false and thus are left wondering how could such an unrealistic theory be so very accurate in its predictions.

One popular interpretation of the neutral theory is that it is simply a “null model.” Hubbell’s theory assumes that certain causal processes are absent and in due course it will be rejected insofar as it cannot accurately predict some phenomena of interest. In fact, this is an interpretation at times Hubbell himself

¹ I thank Michael Strevens, Ken Waters, and Jim Woodward for providing helpful comments on the manuscript (and to Ken and Jim for inviting me to such an excellent workshop). Likewise, I thank Stephen Hubbell for useful correspondence regarding the Neutral Theory of Biodiversity and Biogeography.

has articulated and the history of ecology has served to reinforce. In this essay, I argue that in fact there is a different interpretation one can give of the neutral theory. Specifically, the theory is actually realistic since it represents the relevant causal factors of the phenomena that it purports to explain. Of course, it goes without saying that the neutral theory is probably false and will be replaced – the history of science is littered with false, rejected theories. In fact some ecologists argue that this is so now given newer more exacting tests have been and are being done (McGill 2006). Nevertheless, the neutral theory serves as an important example of a larger philosophical point regarding explanation and causal relevance.

The structure of the essay is as follows. First, I sketch the traditional niche-assembly framework in which ecologists have tried to explain ecological patterns. In addition, I highlight some of the ways in which it has been challenged. As a consequence of debates over the niche-assembly framework, there has been an emphasis on null hypotheses. In the second section, I consider the equilibrium theory of island biogeography. What is remarkable about this theory is it is one of the first “neutral” theories in community ecology. Third, I consider the neutral theory. Given its status as a remarkably unrealistic but predictively accurate theory, I consider its status as a “null hypothesis.” Finally, I provide an alternative interpretation to this one using a simple account of causal relevance through notions of robustness and also through sketching the kairetic account of explanation of Michael Strevens.

II. The Faltering Niche. Ecologists have noted that often differences between similar species when they co-occur are greater than when they do not co-occur. One possible explanation of “character displacement” is that interspecific competition causes the species to differ when they co-occur. Famously, G. E. Hutchinson (1959) noted that three European insect species *Corixa affinis*, *C. macrocephala*, and *C. punctata* had “segregated distributions.” The larger *C. punctata* occurred with either *C. affinis* or *C. macrocephala* but the smaller two did not co-occur. Hutchinson hypothesized that if species differ in size or life history characteristics they will differ in resource use to avoid competitive exclusion. After some empirical investigations, he suggested coexisting similar species differed in some dimension of size by a factor of 1.3.

Hutchinson provided a formulation of the competitive exclusion principle: if two species share the same niche, then they cannot coexist. In addition, he articulated this principle set-theoretically. Consider every independent factor n that affects a given species’ abundance and suppose we have an n -dimensional space composed of just those variables. In this space, the non-empty area in which the species persists is the “fundamental niche” of the species. The area in which the species can persist when we include interspecific interactions is the “realized niche” of the species. Hutchinson’s reformulation of the competitive exclusion principle then is this: realized niches of different species do not intersect.

Consider an example of an empirical evaluation of the competitive exclusion principle. At the suggestion of Hutchinson, Robert H. MacArthur

conducted his classic study of competitive exclusion amongst five warbler species in Maine (MacArthur 1955). What MacArthur found was that where competition would be most likely to occur, there was a remarkable degree of niche specificity. Some species fed high in the tree, some on the forest floor, some fed near tree trunks, and others would forage on the branches. MacArthur's careful empirical work confirmed the competitive exclusion principle.

So, the competitive exclusion principle claims if several species occupy the same niche, then they cannot coexist. But, species will rarely share *exactly* the same niche; their resources requirements will invariably differ. Thus, as stated, the competitive exclusion principle is trivial. The right question seems to be how much "niche overlap" can occur with coexistence? MacArthur and his colleagues Richard Levins (1967), Henry Horn (1972), and Robert May (1972) addressed these questions quantitatively. Here we will consider May and MacArthur's treatment of the issue.

Let's start with a niche with one dimension x – say food size – and we will consider for each value of x how a set of species will utilize food of that size. Ecologists term this a "resource spectrum." For any species, let suppose it has a "preferred size" represented by the mean and some dispersion about that mean. We will let d be the distance between adjacent means, w is the dispersion around the mean for a given species, and K is the amount of food consumed as some function of food size. May and MacArthur posited the ratio d/w as a measure of niche overlap. Graphically, we can depict this as follows.

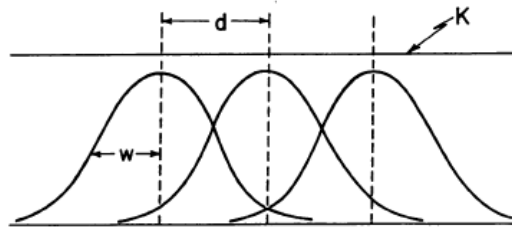


Figure 1. A resource spectrum containing three species whose resource utilization function is characterized by a separation d between means and standard deviation w (May and MacArthur 1972, 1109).

Using a traditional Lotka-Volterra model, May and MacArthur concluded that in the deterministic case where parameters are constant, there is no limit to how many species can be “packed” on the resource spectrum. However, if environmental fluctuations (“white noise”) are incorporated into the species’ K respectively, then there is a limit to the number of species that can be packed along the spectrum. They write,

We observe that the species packing parameter d indeed goes to zero when the environmental variance becomes strictly zero, but that for any finite environmental variance, d remains roughly equal to the utilization function width, w . (1972, 1109)

They concluded that in a fluctuating environment in which the community is stable, adjacent species must be separated by $d/w \approx 1$. Intuitively, when $d > w$, then there is too little overlap and when $d < w$, there is too much overlap. Additionally, they claimed that there was some empirical evidence for this rule (May and MacArthur 1972, 1112).

Subsequently, May and MacArthur’s work on limiting similarity came under serious criticism. First, Peter Abrams argued their result was not robust (1983). For example, the formula for determining the competition coefficients

can be derived from consumer-resource equations that assume the functional response of the consumer species is linear where the resource itself grows logistically. However, neither of these assumptions is realistic. Additionally, the model unrealistically assumes that the environmental variability affecting different species is uncorrelated.

Second, many ecologists thought that limiting similarity as a pattern to be explained was simply an “artifact.” Henry Horn and Robert May (1977) humorously noted many objects exhibit a 1.3 difference in ratios (e. g. musical instruments in an orchestra). However, the most serious critique along these lines came from what has been termed the “null hypothesis debate.” Essentially, it involved a debate regarding how ecological theory should be tested and when should causal processes be postulated to explain phenomena of interest.

In 1975, one of MacArthur’s collaborators Jared Diamond published work on the distribution of bird species in the Bismarck Archipelago near New Guinea (Diamond 1975). Similar to the research of Hutchinson and MacArthur, he claimed that certain combinations of species never appeared together in the archipelago. For example, two species of cuckoo-dove *Macropygia nigriostris* and *M. mackinlayi* never occurred on the same island but appeared separately with them occupying six and fourteen islands respectively and there were thirteen islands not occupied by either. Diamond argued that the probability of these two species not co-occurring together given that they were randomly distributed was very improbable. He hypothesized that this “checkerboard pattern” resulted from interspecific competition.

In response, Edward Connor and Daniel Simberloff (1979) argued that Diamond's study was problematic since this checkerboard pattern could arise from random colonization instead of competition. Suppose that the *Macropygia* doves consists in two species M and N such that M is on 14 islands, N is on 6 distinct islands, and 13 other surveyed islands have neither species present. Then, the probability of this arrangement randomly distributed over the 33 islands is $\binom{33}{14}\binom{19}{6} / \binom{33}{14}\binom{33}{6} = .0245$ (Connor and Simberloff 1979, 1133). So, if

we suppose the probability of these two species co-occurring is approximately 1/40, then this does seem improbable. However, they write,

When one recalls that there are $\binom{141}{2} = 9870$ pairs of birds in the Bismarcks, it is clear from the above probabilities that by chance alone certain species pairs would not occur together on any island. What one wants to know is how many such pairs, trios, etc. would be expected for randomly distributed birds, and how many such pairs, trios, etc. are actually observed. (ibid, 1133)

Given that Diamond had not made his Bismarck Archipelago data available, they then provided a "null model" that randomized the 211 species in the West Indies in their sample several times and found of the 22,155 possible pairs of species on average 12,448 had disjunctive distributions such as Diamond found. Given that the actual distribution of amongst pairs of species with disjunctive distributions was 12,757, they concluded that one could not conclude interspecific competition determined the species distributions (ibid, 1134, 1135). They recommended that "null hypotheses" should be formulated and rejected

before causal processes are postulated to explain certain patterns.

Connor and Simberloff constructed these null models of communities keeping certain properties present and removing others. For example, they proposed keeping the number of species per island, the relative abundances of species, and their incidence functions (the probability of a species occurring on an island given the total number of species on that island) but removing the presence of interspecific competition by randomizing the other properties. If the null hypothesis and actual data differed in a statistically significant manner, then the null hypothesis is rejected and competition suggested. Defenders of this self-styled Popperian approach argued that these null hypotheses are more parsimonious and should be tested prior to interspecific competition hypotheses.

In response, critics claimed the hypotheses Simberloff and his group proposed were not in fact genuine null hypotheses. In Neyman-Pearson testing, a null hypothesis and alternate hypotheses are mutually exclusive and exhaustive. However, Michael Gilpin and Diamond argued the nulls were in fact compatible with competition hypotheses. For example, the properties retained in the null hypotheses – the species pools, dispersion abilities, and “incidence functions” – could be the result of the “ghost of competition past” (Gilpin and Diamond 1983). Second, Connor and Simberloff were using groups of species not restricted to guilds (i. e. groups that utilize similar resources) and interspecific competition only occurs between species in the same guild (Gilpin and Diamond 1983). Connor and Simberloff responded *even if* they only used

species from the same guild, a “checkerboard pattern” was not indicative of competition and furthermore Gilpin and Diamond had not provided evidence of “ghost of competition past” (Strong et. al. 1984). The null hypothesis debate was “rough and tumble” but it forced ecologists to think hard about how theory should be evaluated. Importantly, as we shall see, it is part of the background against which Hubbell’s neutral theory appears.

It is important to note that Connor and Simberloff’s notion of a null hypothesis is not simply that found in the Neyman-Pearson framework of statistical hypothesis testing. According to a simplified version of the latter, we formulate two mutually exclusive and exhaustive hypotheses the null H_0 and the alternate H_1 . Suppose X_1, X_2, \dots, X_n is a random sample collected from a population which we assume is normally distributed with a mean μ and standard deviation σ . Furthermore, suppose we calculate the sample average \bar{x} , the sample standard deviation s , and find choose an appropriate test statistic. To test the null hypothesis that $H_0: \mu = \mu^*$ where μ^* is a hypothesized value, we calculate our test statistic to see if it is inside or outside an interval $(-a, a)$ such that $P(-a < T < a) = 0.95$. If it is outside, then we reject the hypothesis at the 5% significance level otherwise we accept the hypothesis. Thus, in the case above, we are comparing randomly distributed disjunctive distributions of bird species versus those observed in the West Indies. Connor and Simberloff however have provided a *null model*. On the basis of their model, they claim the checkerboard distribution need not result from interspecific competition. However, their null hypothesis is not simply that the checkerboard pattern could have arisen by

“mere chance” but rather that their null model, which may make process assumptions, is consistent with the checkboard pattern (Simberloff 1983, Colwell and Winkler 1984). Thus, when ecologists use the term ‘null hypothesis,’ it may refer to a “null model” that excludes a given particular causal process but may include assumptions regarding alternative causal processes of its own. As Nicholas Gotelli and Gary Graves write,

A null model is a pattern-generating model that is based on randomization of ecological data or random sampling from a known or imagined distribution. The null model is designed with respect to some ecological or evolutionary process of interest. Certain elements of the data are held constant and others are allowed to vary stochastically to create new assemblage patterns. The randomization is designed to produce a pattern that would be expected in the absence of a particular ecological mechanism. (1996, 3 – 4)²

Thus, null hypotheses as discussed by ecologists need not simply be claims regarding whether differences between population parameters are statistically significant but can be models excluding certain causal processes but which includes others.³

By way of summary, we began with a very simple hypothesis: if species have identical niches, then they cannot coexist. Of course, this is a trivial claim given that species invariably differ in their niches. Thus, how much niche overlap can occur consistent with coexistence? In response, theoretical ecologists

² Likewise, Gotelli and Graves write, “Null models do not portray the world as ‘having no structure’ or even as being random. Rather, the null hypothesis (for community-wide competition) is that species occurrences are random with respect to one another” (1996, 12). This is consistent with the null model building in lots of biological and ecological structure which goes beyond the Neyman-Pearson framework.

³ Thanks to Ken Waters and Jim Woodward for forcing me to be more explicit in discussing how null hypotheses in Neyman-Pearson statistical hypothesis testing and in community ecology can come apart.

produced a theory that was incredibly complicated and difficult to test. In response, some empirically minded ecologists suggested that before we develop such complicated theories we should “look before we leap.” Do not introduce processes that are unnecessary to explain the relevant patterns. It is crucial to note these null hypotheses need not be process free; rather they may exemplify alternative and possibly preferred processes.

II. The Ironic “Null” Hypothesis. Robert MacArthur was a very formidable theoretician. In addition to his work on limiting similarity, he was also at work on the topic of island biogeography with E. O. Wilson. Here the question is how to explain the distribution and relative abundance of species on islands. Like many others, MacArthur and Wilson noticed two patterns. First, more species are expected on larger islands than on smaller islands. Second, more species are found on islands closer to the mainland than farther away. The former is termed the “area effect” and the latter the “distance effect.” In 1967, MacArthur and Wilson’s monograph on the equilibrium theory of island biogeography appeared. Their model included the following basic assumptions. First, there is an equilibrium number of species on a given island. Second, this stable equilibrium is result of immigration rate from the mainland and the extinction rate on the island. Third, the distance from the mainland solely determines the immigration rate. Fourth, the size of the island solely determines the extinction rate on an island. Finally, though there is a “diversity” stable equilibrium, there is not a “taxonomic” stable equilibrium on an island. This is just to say that the number

of species on an island is stable but the identity of species on the island will change.

Very simply, if we let P represent the number species in our pool, I represent the rate of immigration, E represent the rate of extinction, and \hat{S} represent the stable equilibrium of species on the island, then we can depict the equilibrium model with the following graph.

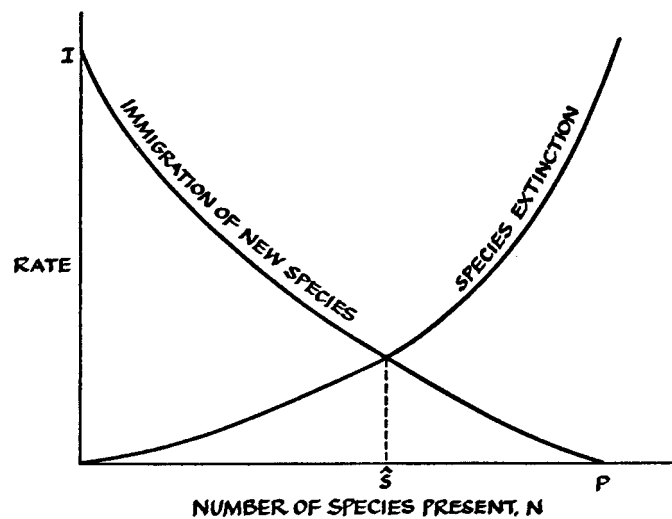


Figure 2. The equilibrium model of species on a single island (MacArthur and Wilson 1967).

Likewise, we can see how the equilibrium number of species varies with different rates of immigration and extinction producing the distance and area effects.

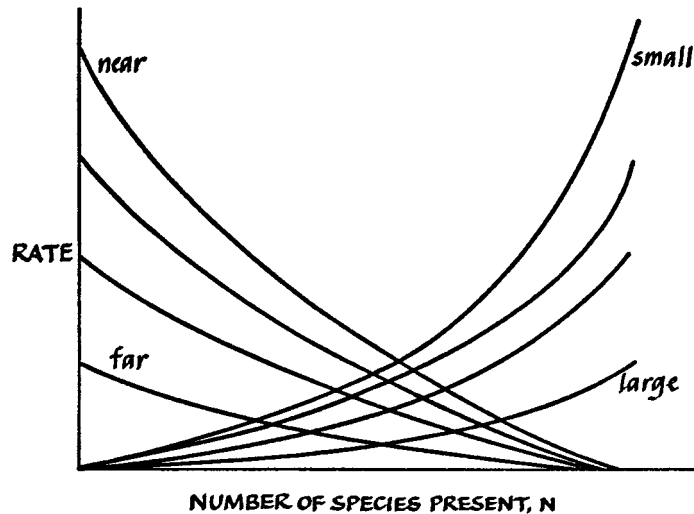


Figure 3. The equilibrium model with varying distances from the mainland and different sized islands (MacArthur and Wilson 1967).

The MacArthur-Wilson model has been tested against a variety of island communities. E. O. Wilson and Daniel Simberloff (while Wilson's graduate student) (1969) conducted experiments in the Florida Keys where there were thousands of mangrove islands that differ in distance from the mainland and in size. By applying methyl bromide defaunating a set of control islands, they could test the equilibrium theory. They found the following. First, species abundances returned to their previous number. Second, species richness was a function of island size and distance. Third, there was substantial species turnover. However, Simberloff (1976) would later realize that the predicted rate of species turnover was too high (since they counted "transient species" as going extinct when they were not).

As one would expect the equilibrium model was oversimplified in a variety of ways. For example, they assumed that distance from the mainland alone determines the rate of immigration and the size of the island alone determines

the extinction rate. Biologists argued that the shorter the distance from the mainland the lower the extinction would be since other members of a given species will probably be on the island. This is termed the “rescue effect.” In addition, they argued that the larger the island the more likely a species will “hit” the island via immigration. This is termed the “target effect.”

Regardless, even if the equilibrium theory is incorrect in certain respects, it provided theoretical resources for investigating patterns regarding islands and mechanisms by which those patterns can be predicted and explained. As MacArthur and Wilson write,

A great deal of faith in the feasibility of a general theory is still required. We do not seriously believe that the particular formulations advanced in the chapters to follow will fit for very long the exacting results of future empirical investigation. We hope instead that they will contribute to the stimulation of new forms of theoretical and empirical studies, which will lead in turn to a stronger general theory and, as R. A. Fisher once put it, “a tradition of mathematical researches upon which a mathematical physicist can draw in the resolution of species difficulties.” (1967, v)

Theoreticians when faced with the possibility of recalcitrant data often provide reflections like these. Their theories provide heuristics in the search for better theories.

As Stephen Hubbell has noted, the equilibrium theory of island biogeography was remarkably powerful but it suffered from several limitations over and above the ones usually cited. First, it assumes species are identical in the immigration and extinction rates. That is, the equilibrium theory is a *neutral theory* at the species level since it assumes that they are ecologically equivalent

and communities are formed by random dispersal. This is ironic since as Hubbell writes,

Thus, the theory is far closer to theories of pure dispersal assembly than to the niche assembly theories of classical ecology, which ironically, MacArthur also championed as the leading ecological theorist of his day (1997, S10).

MacArthur pioneered both niche *and* neutral theories; that is, theories that postulate interspecific competition as the main mechanism driving community assembly versus random dispersal, chance, and history as the main mechanisms (see further discussion in §III). Second, the theory assumes that the source pool is constant and hence no new species appear on the mainland though they may be new species locally on islands. As such, the theory has no mechanism of speciation. Third, the theory does not predict the relative abundance of species but only species richness (i. e. \hat{S}) (1997, S10).

Hubbell, in his previous work but culminating in his 2001 monograph, explicitly builds his theory with MacArthur and Wilson's equilibrium model in the mirror; he sees the neutral theory correcting its deficits. Concurrent with the challenge to niche-assembly theories and the rise of so-called null hypotheses, we see the first presentation of neutrality ironically from a proponent of the former. It is to Hubbell's theory that we now turn.

III. Neutralism or the New Null? According to Hubbell, there are “two conflicting world views” on the nature of ecological communities “which was brought into stark relief by MacArthur and Wilson's theory, although perhaps

only in hindsight” (2001, 8). The first is the *niche-assembly perspective*. As Hubbell describes it,

This view holds that communities are groups of interacting species whose presence or absence and even their relative abundance can be deduced from “assembly rules” that are based on the ecological niches or functional roles of each species (2001, 8).

This program found its theoretical expression in the likes of Hutchinson, MacArthur, Horn, Levins, and May as we have seen. Interspecific competition determines which species are present or absent from a community. On the other hand, there is the *dispersal-assembly perspective*. Hubbell writes,

It asserts that communities are open, nonequilibrium assemblages of species largely thrown together by chance, history, and random dispersal. Species come and go, their presence or absence is dictated by random dispersal and stochastic local extinction. (2001, 8 – 9)

What then is a “neutral” theory in ecology? Hubbell characterizes it as follows:

Thus, the essential defining characteristic of a neutral theory in ecology is not the simplicity of its ecological interaction rules, but rather the complete identity of the ecological interaction rules affecting all organisms on a per capita basis. (2001, 7 italics in original)

Thus, neutrality assumption is that organisms are ecologically equivalent.

Hubbell “modified” the equilibrium theory to arrive at the neutral theory of biodiversity and biogeography. First, speciation is incorporated (through “point mutation” and “fission” models). Second, a theory of relative species abundance is added; specifically a “zero-sum multinomial distribution.” Third, the neutral theory assumes the dynamics of ecological communities is a stochastic, zero-sum game. If a species increases in abundance by one organism, then the other species must decrease by the same amount. Mathematically, this is represented

by $J = \rho A$ where J is the number of individuals of all species in the community occurring at density ρ in area A .⁴

The spatially implicit version of the neutral theory is a Markovian model of the dynamics of an arbitrary species i in a local community which each species obeys the zero-sum assumption.⁵ Here we are concerned with two different scales – that of the local community and that of the metacommunity. Let N_i be the current population size of the i th species, J is the size of the local community (where $J = \sum N_i$), m is the probability that a death in the local community is replaced by an immigrant from the metacommunity source area, and P_i be the relative abundance of the i th species in the metacommunity (with $0 < P_i < 1$).

We can now give a “master equation” describing the transition probabilities for the population decreasing in size by one individual, staying the same size, or increasing by one individual in the next time step.

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

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

⁴ It is worth noting that Hubbell argues for the zero-sum assumption in part by citing empirical data that “...large landscapes are essentially always biotically saturated with individuals of a specified metacommunity or taxon” (2001, 53).

⁵ The spatially implicit theory encodes whether an individual is in the local community as opposed to the metacommunity whereas the spatially explicit theory encodes where every individual is at every time. The results we will consider depend only on the former whereas other results like claims regarding species-area relationships depend on the latter.

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

Consider the first equation. Given our zero-sum assumption, if N_i decreases by one individual, then either immigration from another species occurred from the metacommunity or a local birth in a species other than i occurred. Consider the second equation and assume a death occurs. Supposing the death occurs in N_i , the probability of N_i remaining the same size is given by the immigration of i individual from the metacommunity or a local birth in i . On the other hand, if the death occurs in species other than N_i , then there is immigration of species other than N_i or a birth in a species other than N_i . Finally, consider the third equation. So, the probability of N_i increasing by one individual is given by the probability of an immigration of an individual of i or a local birth in i .

A species i can “ecologically drift” to local extinction where $N_i = 0$ or it can drift to monodominance where $N_i = J$. The exact probability of the i th species being in any particular abundance from 0 to J can be found by solving for the equilibrium eigenvector of the transition matrix for the “master equation” above. The equilibrium abundance of the i th species in the local community is simply the size of the local community J , times the relative abundance P_i in metacommunity of the i th species, or $E\{N_i\} = JP_i$.

Just as we want to know what the equilibrium local community composition is, we would like to know the same regarding the metacommunity. The steady-state in species richness and relative species abundance will occur when there is an equilibrium between speciation and extinction. Let J_M be the

total number of individuals of the source metacommunity (i. e. $J_M = \sum J$) and let v be the probability per birth of a speciation event. To find the equilibrium in the metacommunity, we must determine the unconditional equilibrium probability of every possible configuration of relative species abundance in a sample of J individuals given that it is randomly drawn from our metacommunity. So, let $\theta = 2J_M v$. The probability of obtaining S species with exactly n_1, n_2, \dots, n_S individuals, respectively (where $J = \sum n_i$) is given by,

$$\Pr\{S, n_1, n_2, \dots, n_S\} = \frac{J! \theta^S}{1^{\theta_1} 2^{\theta_2} \dots J^{\theta_J} \theta_1! \theta_2! \dots \theta_J! \prod_{k=1}^J (q + k - 1)}$$

where ϕ_i is the number of species that have i individuals in the sample of size J . Let's rank order our species from commonest to rarest. The expected abundance r_i of the i th-ranked species in the equilibrium rank-ordered relative abundance distribution for a random sample of size J individuals from the metacommunity then is,

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

This equation then provides the expected dominance-diversity curve for the metacommunity when there exists an equilibrium between speciation and extinction. The expected metacommunity abundance of the i th species is given by $P_i = E\{r_i | J\}$. We have combined the theoretical results from the local community and metacommunity and have removed any need for species-specific parameters in the neutral theory.

In Hubbell's neutral theory, θ is a dimensionless number that completely specifies relative species abundance, species-area relationships, and metacommunity diversity at equilibrium. Appropriately, Hubbell calls θ the *fundamental biodiversity number* and it varies from zero to positive infinity. When $\theta = 0$, then there is a single monodominant species everywhere and when $\theta = +\infty$, every new individual sampled is of a new species. We can see this by inspecting the following graph that depicts the expected metacommunity dominance-diversity distributions for a sample of sixty-four individuals for different values of θ (Hubbell 2001, 125).

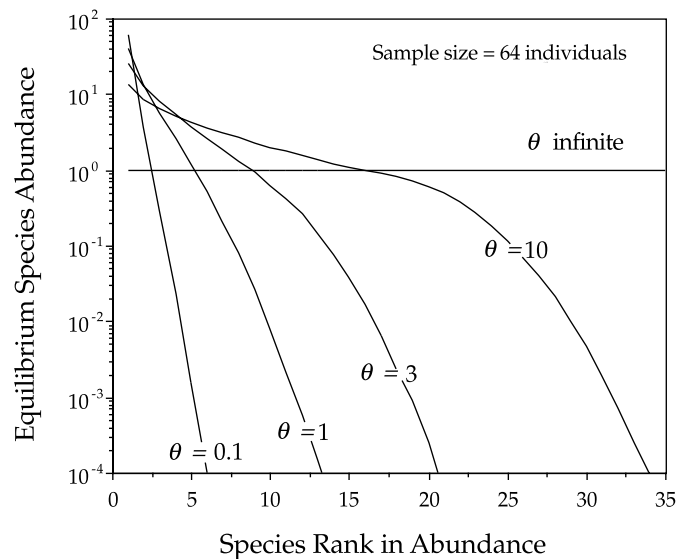


Figure 4. Expected metacommunity dominance-diversity distributions for a sample of 64 individuals, for various values of the parameter θ (2001, 125).

So much for theory, how does the theory stand up to empirical data?

Initially, after publication of Hubbell's book, it did exceptionally well (subsequent testing has complicated things as one would expect). Let's consider just two examples. The first figure depicts the fitted and observed dominance-diversity

distributions for trees > 10cm dbh (diameter at breast height) in a 50 ha plot of moist tropical rainforest on Barro Colorado Island, Panama with a best fit θ value of 50 and $m = 0.1$.

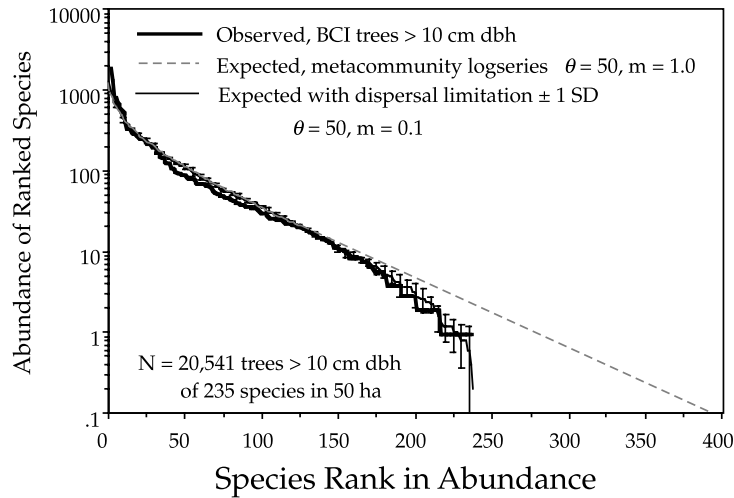


Figure 5. Fitted and observed dominance-diversity distributions for trees on Pasoh Forest Reserve, Malaysia (2001, 138).

In the second graph, we have the fitted and observed dominance-diversity relationships depicted for a 50 ha plot in lowland mixed dipterocarp tropical rainforest in Malaysia. This forest is approximately two and a half times greater in species richness than the forest on Barro Colorado Island. Here we have a best fit θ value of 180 and $m = 0.15$.

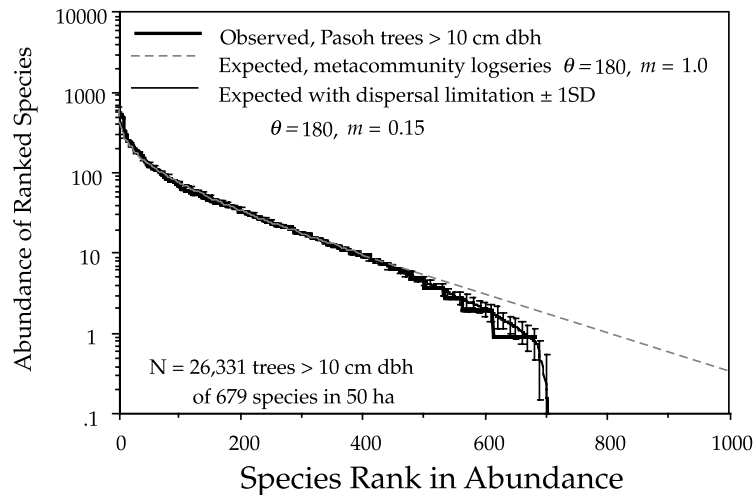


Figure 5. Fitted and observed dominance-diversity distributions for trees on Pasoh Forest Reserve, Malaysia (2001, 138).

In my experience, it is rare to see an ecological theory as predictively accurate as the neutral theory. As Hubbell himself notes, “The goodness of fit of the theoretical distributions to observed dominance-diversity curves is often quite remarkable” (2001, 136). But, we are left with a philosophical conundrum. We know that the theory assumes that every individual in the metacommunity is ecological equivalent – they have the exact same probability of giving birth and dying – and we know this is false. Moreover, we can see that the theory is remarkably accurate in its predictions. How do we reconcile these two if we assume that predictive accuracy is an indicator of truth?

Following the debates over interspecific competition, Hubbell has opted to think of the neutral theory as a “null hypothesis.”

I argue, seemingly paradoxically, that the most rapid path to understanding ecological systems, especially complex systems such as species-rich tropical tree communities, is through an interaction of empirical science, guided by strong inference, with theories that start very simply, with few free parameters and assumptions, and add complexity

reluctantly, kicking and screaming, only when absolutely necessary to obtain some desired level of fit to the data. Neutral theory is one such starting point. (2008, 143)

As we saw in §II, a null hypothesis is not a process free hypothesis regarding pattern; rather, it can be a process model, which ignores certain causal processes under investigation. Essentially, the theory presupposes causal factors like dispersal, speciation, and extinction, which must be operating in any local community or metacommunity. As such, we can rectify the idealization of ecological equivalence only by adding more and more causal factors including differences regarding the niches of species. I however want to resist this interpretation as the only reasonable alternative. In the next section, I will sketch one way of viewing the neutral theory as a realistic, explanatory theory.

IV. The Neutral Theory and Explanatorily Relevant Causal Factors. One account of explanation (or even more minimally, one way in which to explain) is to provide causal information. That is, to explain something is to cite the factors that caused it.⁶ If our explanandum is sufficiently fine-grained, then every factor causally related to it might be required to explain why it is the case. However, when our explanandum is course-grained, not every causal factor is relevant to explaining why it occurred (Strevens 2004). As a slogan, you might put this way: to explain is to cite causally relevant factors.

⁶ This I take it is one of the lessons provided by the classic counterexamples to Carl Hempel's DN model of explanation. Here I will not take a stand as to whether explanation is always and only causal.

It is important to note that there are two ways in which we might “leave out” causally irrelevant factors. One way is to *abstract* in our explanatory theory or model. Here we deliberately omit a property that we take to be irrelevant to the causal goings on by not including a parameter that represents this property. Another way to “leave out” causally irrelevant factors is to *idealize* in our explanatory theory or model. Here we deliberately misrepresent a property or relations amongst properties that we take to be irrelevant to the causal goings on but we do include it in the theory or model. For example, we might model evolutionary change using a simple genotypic model omitting mutation as an evolutionary force. This is abstraction. On the other hand, we might assume that genotypic fitnesses are constants though we know they are not because we do not think that variation in fitness values over time is causally relevant. This is idealization. With regard to Hubbell’s neutral theory, he both abstracts and idealizes; however, the assumption of ecological equivalence is an idealization in the above sense. He includes the properties of mortality and immigration but assumes that mortality and immigration per capita is the same across species.⁷ Nevertheless, even if we agree with this slogan “to explain is to cite causally relevant factors,” we need some account of *causal relevance*. There are many different accounts and I will consider two.⁸

⁷ Thanks to Michael Strevens for bringing to my attention the relevance of abstraction and idealization to my discussion.

⁸ Alternatives that I do not examine include explicating probabilistic relevance and counterfactual dependence.

Let us suppose that theories or models are described by deductively closed sets of propositions (hereafter I will talk mostly of models).⁹ Consider a *family* \mathbf{M} of models where each model M_i has its propositions divided up into two non-empty subsets A and A^C . $A = \{A_1, A_2, \dots, A_n\}$ consists in the set of *shared assumptions* retained in each element of \mathbf{M} . $A^C = \{A_1^C, A_2^C, \dots, A_n^C\}$ is the complement of A which consists in those assumptions that vary between models. Let us call our prediction P and suppose it concerns the values of the variables and parameters. Finally, let us say that two models with A are distinct just in case they contain logically non-equivalent A_i^C and A_j^C assumptions. Last, let us define a notion of *robustness*. Consider a set of models $\mathbf{M} = \{M_1, M_2, \dots, M_n\}$ where each model is composed of A and at least one distinct A_i^C .

A prediction P is *robust* over \mathbf{M} if for each $M_i \in \mathbf{M}$, M_i entails P ; otherwise, it is *fragile*.

We can now articulate the notion of *causal relevance*. Suppose we compare two models M_i and M_j where the former has an assumption A_i^{C+} and the other lacks this assumption or has the assumption A_i^{C-} . Here A_i^{C+} is the assumption that either a causal factor C is present, takes a non-zero value, etc. whereas the assumption A_i^{C-} says either that C is absent, takes zero as its value, etc. Hence,

⁹ Here I am not making a sharp distinction between theories and models. The biologists move between these locutions and so will I. However, I am construing theories and models propositionally for ease of exposition. Everything that I say here could be expressed in the semantic view of theories for example. In addition, the account of *robustness* is derived from Odenbaugh (2011).

we can include both abstraction and idealization in our account of robustness.

Thus,

C is *causally irrelevant* to *P* if *P* is robust over $\mathbf{M} = \{M_i, M_j\}$.

And

C is *causally relevant* to *P* if *P* is fragile over $\mathbf{M} = \{M_i, M_j\}$.

That is, *C* is causally irrelevant to *P* if adding or removing *C* from our model doesn't alter whether *P* is implied. Likewise, *C* is causally relevant to *P* if adding or removing *C* to our model does alter whether our model implies *P*. So, causal relevance presupposes that a prediction is not robust over the appropriate set of models.

Obviously, there are limitations to this way of conceptualizing causal relevance. First, we are considering predictions that are logically entailed by models. Hence, "probabilistic implications" are left out (however, see Strevens (2008)). Second, we are assuming that if A_i^{C+} is removed from M_i and thus M_i does not imply *P*, then there is a causal relationship between the causal factor A_i^{C+} and explanandum *P*. One might argue that there are entailments that fail when A_i^{C+} is removed but they do not represent causal relationships. An attempt to provide a far richer account of causal relevance occurs in Michael Strevens's work (2004, 2008).

Strevens's kairetic account is an attempt to blend causal and unification accounts of explanation; however, the resulting theory remains thoroughly causal.

Despite its borrowing from the unification account, the kairetic account is not a hybrid account of explanation, but a fully causal account: the technical apparatus of the unification approach is appropriated not for its ability to capture the notion of unification, but rather, for its ability—quite unintended by its creators—to capture a notion crucial to the causal account, namely, the notion of difference-making. (2004, 154)

On the unification approach, we explain an explanandum by deriving it from a theory thus showing that it is part of a general pattern. The unification approach does well “since it does not aim for causal accuracy, but rather for a kind of generality that may well be enhanced by omitting or changing the details” (ibid, 157).

However, as we noted, even on a causal approach to explanation, not every causal fact is explanatory. Strevens writes,

I propose that the explanatorily relevant parts of any causal network are the elements that made a difference to whether or not the explanandum occurred. It is important to note the whether or not. To be explanatorily relevant, a causal factor must not merely make a difference to how the explanandum occurred; it must make a difference large enough to bear on whether or not it occurred at all. (ibid, 158)

Stevens articulates his own Modified Classical Approach to Difference-Making which can be summarized as follows: C is a cause of E iff C is an insufficient but non-redundant part of an unnecessary but sufficient condition for E . Put more succinctly, C is an essential part of some set of actual conditions jointly sufficient for E . J. L. Mackie originally proposed his INUS account knowing that “sufficiency” is itself a causal notion. Stevens however is not trying to provide a non-circular account of *cause*.

According to the Modified Classical Account, the difference-makers for an explanandum E is determined by:

1. Take the causal web in which E is embedded and find a set of actual initial conditions and laws that is sufficient to causally produce E (a *veridical deterministic causal model* for E).
2. Remove anything from the causal model that is not necessary for the causal production of E (assuming the model is a set of propositions, this means removing everything from the model that is not necessary for the entailment of E). (2004, 163).

We have Mackie's non-redundant parts of a sufficient condition for E . Each corresponds to an insufficient but non-redundant part of the sufficient condition. This is the *eliminative procedure* for determining difference-makers, and so for determining explanatory relevance and the result is an *explanatory kernel* for E . It is crucial to note that the entailment relation represents the causal production relation but of course not every logical entailment is a causal relation (see the objection raised regarding the simple account of causal relevance above). An event or law C qualifies as a difference-maker for an event E if, and only if, C appears in a kernel for E . That is, there is some veridical causal model for E in which C appears and from which C is not removed by step (2) of the eliminative procedure.

It should be noted that many plausible accounts of causal relevance would reach similar conclusions as the ones mentioned above. For example, within a counterfactual framework one might say that C is *irrelevant* to E if alterations or interventions to C were to occur and yet there were no (or no significant) changes in E ; otherwise, C is *relevant* to E .¹⁰

We can now apply the simple account of causal relevance or Strevens's

¹⁰ Thanks to Jim Woodward for drawing my attention to this point.

kairetic account to the Neutral theory. Recall that neutral model implies there is a stable equilibrium in the local community resulting from balance between immigration and extinction. Likewise, the neutral model implies there is a stable equilibrium in the metacommunity resulting from a balance between speciation and extinction. We can rank-order species and compare an expected and observed relative species abundances. There are a variety of causal factors explicitly mentioned in the neutral theory including birth, immigration, extinction, and speciation (and are parts of explanatory kernels for observed relative species abundances). However, one causal factor that is omitted (i.e., idealized as opposed to abstracted) is niche differences. Thus, using our simple account of causal relevance, since we have a model that implies our explanandum absent this putative causal factor, it appears that it is not causally relevant to the explanandum to be explained.¹¹ That is, given that the neutral theory with the causal factors it describes correctly implies the rank-ordered relative species abundances in tropical rainforests, then adding niche differences would be causally, and hence explanatorily, irrelevant.

Of course, there are niche differences between species. This is obvious as Brian McGill notes when he writes,

Neutral theories of biodiversity assert that all individuals of all species are competitively identical. Any variation in traits between species has no impact on their overall abundance or on their speciation rates. This contradicts 100 years of community ecology. (2006, 1411)

¹¹ Strictly speaking, I am assuming that the other causal factors including immigration, extinction, and speciation are difference-makers and could not be eliminated. In his book, Hubbell considers other even more minimal neutral models and concludes they are simply insufficient to generate the predictions of interest and generate false predictions of their own (2001, Chapter 3).

However, just because there are niche differences between species it doesn't follow that those differences are explanatorily important in understanding phenomena like relative species abundances in communities. Consider the following inference. The neutral theory says that species are ecologically equivalent. But, species are not ecologically equivalent. Hence, the neutral theory is explanatorily incomplete. The conclusion doesn't follow from the premises since a theory is explanatorily complete on a causal account like the ones mentioned above only if it cites *causally relevant factors*. Even if there are niche differences it doesn't follow they are explanatorily relevant.

How can niche differences be causal irrelevant to patterns like relative species abundances? My own view is that a causal factor can be relevant at one scale and not at another. That is, causal relations are *scale-relevant*.¹² Hubbell himself implicitly notes this I think when he writes,

Biogeographers and community ecologists typically work on very different spatial and temporal scales, and therefore it is hardly surprising that their theories for how biotas and ecological communities are assembled should differ. Ecologists tend to focus on small-scale processes shaping the interactions of individuals and populations. They tend to be impressed by the strength and importance of species interactions and of niche differences in stabilizing species assemblages in particular locations. Biogeographers, on the other hand, focus on much larger scale processes and ask questions about migration and range and speciation and extinction in space and time. (1997, S09)

¹² It is interesting as to why a given property P would be causally relevant to a property Q but say P^* is not. One possible answer would be from the way in which objects are composed of parts. Ed Grumbine writes, "A single grizzly has a genetic identity but not a birth-death ratio. A grizzly population has a demographic ratio of birth to deaths but does not have an index of species diversity. An old growth forest contains numerous species but, by itself, exhibits no biological corridors across landscapes" (Grumbine 1993, 25). The genome of a grizzly or demography of grizzlies might simply be spatially and temporally insignificant to landscape patterns.

The sort processes that ecologists traditionally thought governed ecological communities such as interspecific competition certainly can and do affect phenomena on certain spatiotemporal scales, but one lesson of the neutral theory is that they need not be causally relevant when we consider metacommunities and landscapes.

Thus, many ecologists have thought of the neutral theory as a kind of null hypothesis. It essentially tells you what to expect when there are no differences in the demographic properties of species. Given of course that there are such differences we can then build more and more complicated models to predict and explain the phenomena. This is a perfectly reasonable interpretation; however, I have argued that it sells the neutral theory short. It possible that the neutral theory might assume falsely that species are ecologically equivalent but explain a suite of ecological patterns nevertheless because ecological differences are irrelevant to these patterns. As entrepreneur Walter Kidde noted, “Judicious omission is preferable to correct superfluity.”

V. Conclusion. In this essay, I have sketched the niche-assembly perspective via the work done on interspecific competition and importance placed on null hypotheses. Second, I turned to the first neutral theory – that of the equilibrium theory of island biogeography – which served as template for the Stephen Hubbell’s unified neutral theory. Third, I presented the neutral theory and some of its empirical successes. Finally, as many critics have noted, Hubbell’s theory even if predictively accurate assumes that there are no ecological differences

between individuals of a metacommunity, which is clearly false. However, I argued that insofar as we are considering the explanations offered by the neutral theory, the demographic differences properties of individuals don't make a difference. Hubbell was correct to ignore them. A false theory can provide a correct causal explanation.

Bibliography

- Abrams, P. (1983) "The Theory of Limiting Similarity" *Annual Review of Ecology and Systematics* 4: 359 – 76.
- Colwell, R. K. and D. W. Winkler (1984), "A Null Model for Null Models in Biogeography," in Donald Strong, Daniel Simberloff, L. G. Abele, and A. B. Thistle (eds.), *Ecological Communities: Conceptual Issues and the Evidence*. Princeton, NJ: Princeton University Press.
- Connor, E. F., and Daniel Simberloff (1979), "The Assembly of Species Communities: Chance or Competition'?" *Ecology* 60: 1132-1140.
- Diamond, Jared (1975), "Assembly of Species Communities," in M. L. Cody and J. M. Diamond (eds.), *Ecology and Evolution of Communities*. Cambridge, MA: Belknap Press of Harvard University Press.
- Gilpin, Michael, and Jared Diamond (1983), "Are Species Co-occurrences on Islands Non-Random, and Are Null Hypotheses Useful in Community Ecology'?" in Donald Strong, Daniel Simberloff, L. G. Abele, and A. B. Thistle (eds.), *Ecological Communities: Conceptual Issues and the Evidence*. Princeton, NJ: Princeton University Press.
- Gotelli, N. J. and G. R. Graves. (1996) *Null Models in Ecology*. Smithsonian Institution Press.
- Grumbine, E. (1993) *Ghost Bears: Exploring the Biodiversity Crisis*. Island Press.
- Hubbell, S. (1997), "A Unified Theory of Biogeography and Relative Species Abundance and its Application to Tropical Rain Forests and Coral Reefs. *Coral Reefs* 16: S9-S21.
- _____. (2001) *The Unified Neutral Theory of Biodiversity and Biogeography*. Princeton University Press.
- _____. (2008) "Approaching Ecological Complexity from the Perspective of Symmetric Neutral Theory," In *Tropical Forest Community Ecology* (eds.) E. Carson and S. Schnitzer, Wiley Press.
- Hutchinson, G. E. (1957) "Concluding Remarks," *Population Biology Animal Ecology and Demography, Cold Spring Harbor Symposia on Quantitative Biology* 22:415-427.
- _____. (1958) "Homage to Santa Rosa, or Why are There So Many Kinds of Species?" *The American Naturalist* 93: 145-159.

- MacArthur, R. (1958) "Population ecology of some warblers of northeastern coniferous forests," *Ecology* 39: 599-619.
- MacArthur, R. and H. Horn (1972) "Competition among fugitive species in a harlequin environment," *Ecology* 53: 749-752.
- MacArthur, R. and R. Levins (1967) "The limiting similarity, convergence and divergence of coexisting species," *American Naturalist* 101: 377-385,
- MacArthur, R. and R. May (1972) "Niche overlap as a function of environmental variability," *Proc. Nat. Acad. Sci. USA* 69: 1109- 1113.
- MacArthur, R. and E. O. Wilson (1963) "An equilibrium theory of insular zoogeography," *Evolution* 17: 373-387.
- _____. (1967) *The Theory of Island Biogeography*. Princeton University Press.
- McGill, B. (2006) "Empirical Evaluation of Neutral Theory," *Ecology* 87: 1311 – 1423.
- Odenbaugh, J. (2011) "True Lies: Realism, Robustness, and Models," *Philosophy of Science* 78 (5): 1177-88.
- Simberloff, D. (1974) "Equilibrium Theory of Island Biogeography," *Annual Review of Ecology and Systematics* 5: 161-82.
- _____. (1976) "Species Turnover and Equilibrium Island Biogeography," *Science* 194: 572-8.
- _____. (1983) "Competition Theory, Hypothesis-Testing, and other Community Ecological Buzzwords," *American Naturalist* 122: 626 – 635.
- Simberloff, D. and Wilson, E. O. (1969) "Experimental Zoogeography of Islands: The Colonization of Empty Islands," *Ecology* 50: 278-96.
- Strevens, M. (2004) "The Causal and Unification Accounts of Explanation Unified – Causally," *Noûs*, 38: 154 – 176.
- _____. (2008) *Depth*. Harvard University Press.