The coherence problem with the Unified Neutral Theory of Biodiversity

James S. Clark

Nicholas School of the Environment, Department of Biology, Department of Statistical Science, Duke University, Durham, NC 27708, USA

The Unified Neutral Theory of Biodiversity (UNTB), proposed as an alternative to niche theory, has been viewed as a theory that species coexist without niche differences, without fitness differences, or with equal probability of success. Support is claimed when models lacking species differences predict highly aggregated metrics, such as species abundance distributions (SADs) or species area distributions (SARs). Here, I summarize why UNTB generates confusion, and is not actually relevant to niche theory (i.e. an explanation for why and how many species coexist). Equal probability is not a theory, but lack of one; it does not include or exclude any process relevant to coexistence of competitors. Models lacking explicit species can make useful predictions, but this does not support neutral theory. I provide s suggestions that could help reduce confusion generated by the debate.

The UNTB is not a null model for niche differences

Proponents of the Unified Neutral Theory of Biodiversity (UNTB [1] describe its history as 'controversial'. Despite this recognition, there has not been much real discussion of the issues by proponents. Advocates do not dwell on literature that rejects the UNTB, focusing instead on UNTB predictions of species abundance distributions (SADs or other highly aggregated summaries. Here, I provide a perspective on this history as one who is a critic, but not to balance the perceived successes of proponents with a review of failures. I think more progress can come from highlighting where the confusion lies, what perpetuates it and steps that can be taken to move beyond it. The continuing confusion comes from misidentifying what is controversial and the fundamental coherence problem with UNTB. Rather than review the UNTB history I use some recent examples to highlight how confusion can perpetuate.

The debate is not as hard to resolve as the literature suggests. There are simple steps that can be taken to steer the debate in a productive direction, but it has to start with proponents showing that they can respond to empirical and theoretical problems raised repeatedly in a large literature. I provide several suggestions following a summary of coherence and how it is being sidestepped with debate focusing on issues that are not controversial.

The coherence problem

The 'coherence problem' is a term I will use for the issues raised in [2] and [3]. This is not the same problem that has led others to reject UNTB; it is not about the fact that predictions are incorrect ([4–8]), not diagnostic of anything ([9–11]) or simply implausible [12]. Proponents counter these problems with the claim that UNTB is still a useful null model, as a description of what would happen if species really were the same. This argument is incoherent, because neutral models do not include or exclude niche differences.

The coherence problem is this: contrary to claims, neutral models do not assume that species occupy the same niche, have the same fitness or are the same in any sense; UNTB has nothing to say about how species differences affect diversity. Niche and neutral models differ only in terms of how the random elements in models are interpreted [2]. When individuals or species are assigned the same probability of success in a model, there is no basis for the claim that they occupy the same niche (Box 1). A niche model might generate niches randomly in space and time and then allocate those niches to species. Neutral models pick an individual to succeed at random or pick individuals at random to occupy sites. These terms 'sites' versus 'niches' are two different terms for 'success' (Figure 1) that are applied to models that make no distinction about why or how an individual occupies a site.

When species are at the same relative abundance, assigning identical parameter values to species in stochastic models allocates to each species on average $1/K$ of the total K niches or sites. When species have different abundances, the probability is weighted by relative abundance, because birth rates are assumed to scale with abundance. Drift is slow, not because species are the same, but rather because the average number of 'niches', 'sites' or 'success' opportunities for each species is the same, changing only as they change in abundance. Rather than make species the same, neutral models provide maximum success opportunities to each species. The fraction of sites a species wins depends on specific assumptions of a given model (e.g. a birth–death process or lottery). However, with respect to species differences, such models have nothing to say about the underlying cause (Box 1).

Models that generate 'niches' at random or assign species to 'sites' at random do not represent different processes. They are not two alternative models, one 'niches-for-all', the other 'niches-for-none'. The subjective probability interpretation of a neutral model ('each species could win with probability $p = 1/K'$) is not a statement of equivalence; it describes the state of maximum uncertainty. (For an event with K potential outcomes, complete ignorance is $p = 1/K$.)

Corresponding author: Clark, J.S. (jimclark@duke.edu).

 0169-5347/$ – see front matter doi:10.1016/j.tree.2012.02.001 Trends in Ecology and Evolution, April 2012, Vol. 27, No. 4

Box 1. Neutral models are not even null

Neutral theory has become inaccessible to many ecologists owing to a perceived technical complexity that few are willing to wade through. In fact, the basic concepts behind assumptions and predictions can be stated simply. Here, I show how these assumptions have no bearing on whether species are the same.

An ecologist constructs a model for interactions between species j' and j''. There are K species, but the basic ideas are illustrated by focusing on just these two. If the ecologist is a Neutralist, they write a model for equal probabilities of all propagules occupying a site in a landscape that supports a total of N individuals. The probability that an individual of species j' wins a site could be proportional to its density $n_{j'}$ (Eqn I)

$$p(s_{j'}) = \frac{n_{j'}}{N} \qquad [I]$$

When the species are assumed to have the same average abundance, and the landscape is large, this proportion tends to Eqn II:

$$p(s_{j'}) = \frac{1}{K} \qquad [II]$$

A Niche ecologist imagines niche differences, a niche k for each of K species. Niche labels are generated at random with equal probability, and species j' wins on its own niche, when $k' = j'$. Then (Eqn III):

$$p(s_{j'}) = \sum_{k=1}^{K} I(k = k')\, p(k) = \frac{1}{K} \qquad [III]$$

where $I()$ is the indicator, equal to 1 when its argument is true, and zero otherwise. This is the same answer arrived at by the Neutralist.

Another type of Neutralist assumes that species occupy the same niche, where species j' and j'' can both occupy niches labeled k' and k'', respectively. Retaining the assumption that niches are generated with equal probability (Eqn IV),

$$p(k') = p(k'') = \frac{1}{K} \qquad [IV]$$

The probability of both sites is the same is Eqn V:

$$p(s_{j'}) = p(s_{j''}) = \sum_{k=1}^{K} I((k = k') \cap (k = k''))\, p(k) = \frac{2}{K} \qquad [V]$$

This is a problem, because two individuals cannot occupy the site, so another rule is needed to determine whether to award a site labeled k' or k'' to j' or to j''. Because this Neutralist is unwilling to state why one or the other species might win the site, the assumption of no information means that the outcome is decided by coin toss, with probability 1/2 that sites k' and k'' go to j'. So the indicator function must be stochasticized, being replaced by a probability (Eqn VI),

$$p(j|k') = p(j|k'') = p(j'|k') = p(j''|k'') = 1/2 \qquad [VI]$$

With this change, one determines that the probability that j' obtains the site is (Eqn VII):

$$p(s_{j'}) = \sum_{k \in \{k', k'\}} \frac{1}{2} \times \frac{1}{K} = 2\left(\frac{1}{2} \times \frac{1}{K}\right) = \frac{1}{K} \qquad [VII]$$

So all three models yield the same answer. This basic idea explains why Chisholm and Pacala [18] find that 'niche' and 'neutral' models give the same answers on large landscapes.

The fact that models based on seemingly opposite assumptions about 'niche versus neutral' in Box 1 all yield the same answer is less important than their lack of relevance to the question at hand: how competing species can coexist. The first 'neutral' model of equal probability makes no assumption about how individuals win sites. It does not include or exclude species differences or any specific mechanism. It is not a null model for species being the same. It is not a null model for absence of a mechanism; it is ignorance of the mechanism.

The 'niche' model in Box 1 simply translates ignorance about species to ignorance about sites. This model could apply to the case where j' always outcompetes all other species on its own niche, but it also applies when there is no competition at all. An ecologist might view this as a model for suitable habitat, where two species never encounter one another. The two species could be terrestrial and aquatic, occupying sites that are dry or wet. This model does nothing more than relabel niche k with species j. Because there is no distinction between competition or not, it does not shed light on coexistence. Traditional niche theory has already answered the question about what happens when species do not compete at all. Niche theory is occupied with the more important question of the coexistence of species that do compete.

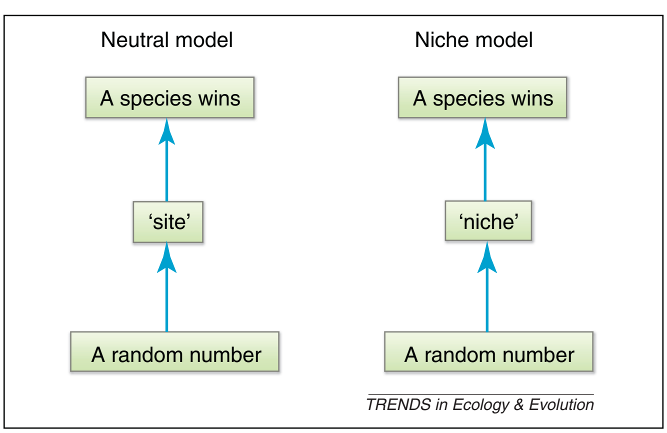

Figure 1. Models used to test neutral theory do not assume that species are the same, only that success is assigned for unknown reasons. 'Niche' or 'site' are terms for success in models that make no distinction regarding mechanisms of coexistence (Box 1).

The second neutral model in Box 1, where there is an attempt to build in both sameness and niche differences, highlights the futility of the exercise. Once attempts are made to make species ecologically the same, the neutral assumption of ignorance forces the admission that the outcome will be determined by unknown differences. When it comes to the two species that are viewed as ecologically the same, stochasticity is used to introduce differences into the model. UNTB is not based on a coherent argument; it is not a null model for niche differences, and 'equal probability' is not a unified theory.

Proponents of UNTB cite Clark *et al.* [2] and/or Clark [3], but do not mention the problem with coherence. Instead, recent debate suggests that use of simple models is controversial. An apparent controversy over the role of simple models masks the real problem, an underlying lack of coherence.

What is controversial?

Proponents describe the UNTB as 'controversial', not to address the refutations of UNTB, but to debate instead whether models need to include species differences explicitly. Here, I summarize with several examples how the debate has become a distraction.

In a paper arguing for the importance of UNTB for conservation, Halley and Iwasa [13] say 'Clark (2009) argues that ecological uncertainty is intrinsically high-dimensional and cannot be described by "stochastic elements, perceived as neutral forces"'. The paper they cite argues the opposite; that is, that stochastic elements are the way to model uncertainty. The fact that there are no 'neutral forces' is a second issue, the coherence problem.

It is certainly true that understanding the coexistence of many competitors will require consideration of the fact that species interact in many ways and models that accommodate this fact, a point included in [3]. Disaggregation from the species scale to the individual scales confirmed that coexistence is high dimensional, showing that competition is concentrated within species despite not being apparent in species aggregate parameters [14]. Subsequent analysis shows many of the variables responsible for these differences, and it does involve larger models [15]. The fact that many factors contribute to coexistence should not be controversial [16]. I have never heard an ecologist say that all models must include species.

Each new model that yields a plausible result without accounting for species differences need not generate debate. Halley and Iwasa [13] found that extinction times are shorter on small forest fragments and on small islands than on large ones. This concept from traditional biogeography is certainly relevant to conservation. At least since classic island-biogeography theory [17], simple models have illustrated useful conservation principles and have contributed to productive debates on reserve design.

Halley and Iwasa's study [13] stands on its own. It does not need UNTB, neither does it support it. Nothing in their analysis shows that the species that went extinct fast were the same as those that did not. It does not show that these species occupy the same niche or have the same fitness (i.e. the logic that sets UNTB apart). It just shows that simple models can capture some general patterns. Proponents co-opt a legacy of simple models in ecology that long pre-dates UNTB, one that is hardly controversial. The apparent controversy about whether simple models can be useful comes at the cost of discussing the real issue, whether an analysis like this can tell whether species are the same. I addressed the incoherence of UNTB, not whether simple models can be useful. Whereas UNTB should not be a part of conservation planning, simple models should always be considered.

Chisholm and Pacala [18] also 'strongly disagree' with Clark [3] on UNTB as a basis for conservation practice. They found that a model where species are assigned sites at random ('neutral') behaves similarly to one where niches are assigned at random, then species are assigned deterministically to their niche ('niche'). To construct a niche model they 'divide the metacommunity into K niches...and allow each niche to operate according to its own neutral dynamics, independently of the other $K - 1$ niches. This is equivalent to assigning each spatial location in the metacommunity to a niche assuming that...a vacant location is always captured by an individual with a matching niche'. This is the coherence problem [2,3]; whether the two models are thought of as neutral with respect to niches or neutral species, neither can claim to assume niche differences or lack thereof (Box 1). Their two models are not precisely the same at local scales, but they are effectively the same with respect to species differences (i.e. both are devoid of information). The fact that they have the same behavior should have given pause. Even if authors did not identify this result as part of the coherence problem I have described, it is hard to see how it supports the UNTB as 'a mechanistic model of patterns of relative species abundances and species–area relationships'. If a model viewed as niches-for-none gives the same answer as niches-for-all, how does it support either one? Warren *et al.* [11] showed that a highly competitive interaction (college basketball) displays the same SADs proponents invoke to support UNTB. They recalled MacArthur's [19] comment that such comparisons represent an 'obsolete approach to community ecology'.

The air of controversy promoted in the UNTB literature lends a sense of immediacy to individual papers, but I do not believe that it serves science. Nothing in [13] should be controversial to any ecologist, and results support patterns that have been recognized for decades. None of the successes claimed by proponents support the UNTB notion that species occupy the same niche, have the same fitness, or any other definition of sameness. They are examples of the noncontroversial notion that simple models can be useful.

A pass on coherence

The controversy of UNTB seems less striking to me than the lack of engagement of issues that should have settled claims made by proponents of UNTB long ago. The pass given to UNTB by editors is the most interesting aspect of the UNTB history. Consider a case where a study claimed a relationship between ethnicity and voting records. Subsequent disaggregation revealed that income disparity was the actual cause. Thereafter, studies submitted to social sciences journals claiming the ethnicity–voting relationship would have to address income. If epidemiological data showing a correlation between radon exposure and lung cancer were disaggregated to find that coal mining was the larger risk factor, then subsequent studies would be expected to disaggregate by occupation.

Disaggregating SADs, the primary evidence of UNTB, shows that species are different [4,14], and it is confirmed by a legacy of ecophysiological studies. Contrary to UNTB, the same species tend to be abundant in many locations for reasons that can be tied to ecological differences. Rather than asking authors to disaggregate, there are now examples of the same authors showing that species are different in one paper and arguing that they are the same in another, even when discussing some of the same data sets (e.g. BCI). Are they different or the same? If they are demonstrably different in ways that affect fitness but not SADs, why are SADs still the basis for evaluating models? Journals continue to publish appeals to highly aggregated distributions, omitting the evidence that SADs are not diagnostic of any process and the evidence showing that the species cannot be the same.

Equal probability is not a unified theory

If the UNTB has become nothing more than an assumption that 'all species have equal probability', then it cannot be a theory of biodiversity. This is just a statement of ignorance

Box 2. Equal probability as ignorance, not mechanistic theory

Does the fact that all assumptions lead to 'equal probability' in Box 1 mean that the neutral model is correct [18]? All three represent different ways of representing ignorance. Consider, for example, a Neutral Theory of atmospheric science. A Poisson model of equal probability could fit the distribution for numbers of rainfall events in a month or a year just as well as a numerical weather prediction model based on atmospheric circulation. It would not be correct to conclude from this observation that neutral theory is an explanation for rainfall alternative to atmospheric circulation. It would also not be correct to conclude that the Poisson is a 'null model' for atmospheric circulation. The Poisson model only assumes that there is no information about when, where and why rainfall occurs. It provides no new insight about which processes do or do not influence rainfall. The value of numerical weather prediction is that it helps the understanding of why rainfall occurs and it enables information (e.g. wind and temperature fields) to be incorporated. Atmospheric scientists should not bother with the Neutral Theory, because it is not a null model for any process, it is obviously false and less useful than an actual theory of atmospheric circulation.

about which species can succeed and why. Random assignment of success is not a null model for niche differences. The $p = 1/K$ rule is just a model for no information about when and why a species obtains a site or its success rate, just as the Poisson distribution of precipitation events cannot be used to say whether particular processes do or do not contribute to rainfall (Box 2).

There is widespread confusion about the interpretation of random elements in models, which proponents have been unwilling to confront. To paraphrase a reviewer:

> I now understand that a model that assigns the same probability to all species does not uniquely represent a world in which all species are identical, since it may just as well reflect a world in which species are very different but the modeler doesn't know how. But is it still incorrect to use equal probability to represent a world in which all species are identical?

The problem is that 'equal probability' does not mean 'occupy the same niche'. The utility of a null model comes from the fact that rejection builds evidence for a mechanism. Conversely, failing to reject builds evidence against that mechanism. The many examples showing that UNTB 'predicts' SADs of species with known niche differences is a simple manifestation of the fact that UNTB is not a null model for niche differences. The assumption of equal probability does not include or exclude any mechanisms.

Neutral models do not address the coexistence questions that captured the attention of ecologists throughout the 20th century or the theory that UNTB claimed to replace: why do so many species coexist? Where is the evidence for all of these niches in nature? Ecologists attempting to explain the coexistence of so many competitors on apparently few resources or residing in highly overlapping niche space turned to the problem of how niche space might be partitioned [14,16,20–22]. Theorists knew about immigration and extinction and included it in many models. They also knew that these processes were not enough to explain high diversity. The UNTB claimed to replace niche theory with an alternative that never addressed the problem. UNTB simply assumes all species have equal success implemented in models that cannot help say why. Clearly, if all K species can each claim $1/K$ of the landscape, the niches, or whatever terms are prefered, there is no biodiversity paradox. The question is not whether many potential competitors can succeed (nature shows that they can), but how and why? These questions remain relevant, and UNTB has nothing to say about them.

Engage the real issues, move beyond nonissues

Several steps could be taken by reviewers and editors to reduce the controversy surrounding the UNTB and move to more productive debate.

(i) 'Neutralists' should be required to confront the incoherence of the argument. Analysis of simple models is fine, but models that assign equal success at random do not serve as null models for sameness or identical niche occupancy. They shed no light on how competitors coexist, beyond the insights on the role of dispersal, which do not address the assumption of sameness.

(ii) 'Equal probability' is not a unified theory or a null model for sameness. It describes a state of ignorance.

(iii) A pattern in nature that agrees with a model that lacks species differences is not a victory for UNTB. Models lacking species differences are not controversial, and controversy should not be created to justify them. If UNTB has become a claim that all models do not have to have species differences, then there is no one to argue with. Finding agreement with a model that lacks species does not support the UNTB claim that species occupy the same niche, have the same fitness, or any other definition relevant to coexistence theory.

(iv) Advocacy for conservation practice based on models that assume random speciation and extinction, with each species provided equal probability of success, should justify such models in terms of their benefits over the alternatives. Exploitation of full knowledge does not mean that models need to be complex or even contain species differences. I argued against neutral theory, because it is based on the assumption of ignorance of why species succeed, whereas conservation practice should benefit from full knowledge [2].

Acknowledgments

For comments on the manuscript, I thank Peter Adler, John Halley, Michel Loreau, Peter Morin, Nigel Pitman, Jurgis Sapijanskas, Denis Valle, Robert Warren, Kai Zhu and three anonymous reviewers.

References

1 Hubbell, S.P. (2001) *The Unified Neutral Theory of Biodiversity and Biogeography*, Princeton University Press
2 Clark, J.S. *et al.* (2007) Resolving the biodiversity debate. *Ecol. Lett.* 10, 647–662
3 Clark, J.S. (2009) Beyond neutral science. *Trends Ecol. Evol.* 24, 8–15
4 Pitman, N.C.A. *et al.* (2001) Dominance and distribution of tree species in upper Amazonian terra firme forests. *Ecology* 82, 2101–2117
5 Turnbull, L.A. *et al.* (2005) Niches, rather than neutrality, structure a grassland pioneer guild. *Proc. R. Soc. B: Biol. Sci.* 272, 1357–1364
6 Harpole, W.S. and Tilman, D. (2006) Non-neutral patterns of species abundance in grassland communities. *Ecol. Lett.* 9, 15–23

7 Dornelas, M. *et al.* (2006) Coral reef diversity refutes the neutral theory of biodiversity. *Nature* 440, 80–82
8 Adler, P.B. *et al.* (2010) Coexistence of perennial plants: an embarrassment of niches. *Ecol. Lett.* 13, 1019–1029
9 Nee, S. *et al.* (1991) Lifting the veil on abundance patterns. *Proc. R. Soc. B: Biol. Sci.* 243, 161–163
10 McGill, B.J. (2003) Does Mother Nature really prefer rare species or are log-left skewed SADs a sampling artifact? *Ecol. Lett.* 6, 766–773
11 Warren, R.J., II *et al.* (2011) Universal ecological patterns in college basketball communities. *PLoS ONE* 6, e17342
12 Purves, D.W. and Turbull, L.A. (2010) Different but equal: the implausible assumption at the heart of neutral theory. *J. Anim. Ecol.* 79, 1215–1225
13 Halley, J.M. and Iwasa, Y. (2011) Neutral theory as a predictor of avifaunal extinctions after habitat loss. *Proc. Natl. Acad. Sci. U.S.A.* 108, 2316–2321
14 Clark, J.S. (2010) Individuals and the variation needed for high species diversity. *Science* 327, 1129–1132
15 Clark, J.S. *et al.* (2011) Climate change vulnerability of forest biodiversity: climate and resource tracking of demographic rates. *Global Change Biol.* 17, 1834–1849
16 Hutchinson, G.E. (1957) 'Concluding remarks'. *Cold Spring Harb. Symp. Quant. Biol.* 22, 415–427
17 MacArthur, R.H. and Wilson, E.O. (1967) *The Theory of Island Biogeography*, Princeton University Press
18 Chisholm, R.A. and Pacala, S.W. (2010) Niche and neutral models predict asymptotically equivalent species abundance distributions in high-diversity ecological communities. *Proc. Natl. Acad. Sci. U.S.A.* 107, 15821–15825
19 MacArthur, R.H. (1966) Note on Mrs Pielou's comments. *Ecology* 47, 1074
20 Hutchinson, G.E. (1961) The paradox of the plankton. *Am. Nat.* 95, 137–145
21 Tilman, D. (1982) *Resource Competition and Community Structure*, Princeton University Press
22 Chase, J.M. and Leibold, M.A. (2003) *Ecological Niches: Linking Classical and Contemporary Approaches*, University of Chicago Press