The Neutral - Niche Debate: An Instance of The Classic Holism vs Reductionism Dichotomy

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Abstract

Ecological systems around the world are under threat while theories concerning relative species abundance are essentially in their infancy. If we are to produce good models on which to base better conservation measures we need to solve the long-standing dispute between the unified neutral theory of biodiversity and niche-assembly approaches to relative species abundance, species distribution and other important factors of community structure. Two solutions are possible: A holist solution in which both theories are incorporated into one larger theory or a reductionist solution in which the two theories clash until only one remains standing. The former solution would produce much more fruitful results in terms of scientific progress and applicability to conservationist practices, because it would incorporates both deterministic and stochastic processes into a unified theory and might provide a model to discern which of these factors are the most important under various circumstances.

1. Introduction

In the history of our planet, humans have never before set such high demands on the production capacity of our planet. The effect of our agricultural practices on the natural diversity is huge; whole areas of what used to be rich and diverse ecosystems have now become replaced by monocultures of agricultural crops such as barley, wheat, corn and rice and humans now require about 40% of the total terrestrial production (Tilman, 2000). Due to human interference, biodiversity is now under threat of habitat degradation and fragmentation, overexploitation, a high rate of invasive species and climate change. (Groom, J.G., Meffe, G.K., Carroll, C.R. et al., 2005).

In this context, it is shocking how extremely limited our knowledge of the richness of nature is. For instance, we have named about 1,750,000 living species, but estimates of just how many species there are on the planet range from 10 million to more than 50 million (May, 1988; Wilson, 1992; Gaston and Spicer, 2004). Many species will have probably already been brought to extinction before they even had a name, let alone their function in the ecosystem understood. In this light it seems quite urgent that new theories about biodiversity are developed, for it is urgent that effective precautions are taken to ensure the continued existence of biodiversity on our planet.

This is a thesis about the Unified Neutral Theory of Biodiversity and Biogeography (UNTB); a theory that deals with biodiversity, set in a geographical context. There have been several attempt at constructing a neutral model for biodiversity and biogeography (Etienne and Alonso, 2007) but the most popular version of such a model is the one introduced in 2001 by Stephen P. Hubbell (2001). It has since had a somewhat mixed reception amongst biologists, with proponents including Graham Bell (2006) and Rampal S. Etienne (2005) and critics including Brian Mcgill (2003) and J. Timothy Wootton (2005). It is the goal of this thesis to evaluate UNTB and its criticisms and to show how this discussion is a classical example of the holism/reductionism debate. In resolving the debate around UNTB it is necessary that implicit assumptions about the holism/reductionism debate are made explicit so that it is clear whether proponents and opponents are discussing the same thing, or working from different premises. I will argue that in criticizing UNTB, most, if not all arguments fit into only two categories; either it is not fully appreciated what the goals of UNTB are or an implicit adherence to a strong reductionism is made. I will then argue that this adherence to reductionism in the strong sense is unnecessary and propose a more instrumentalist approach.

2. Theories of biodiversity and relative species abundance

2.1: The united theory of biodiversity

UNTB is a theory that deals with the nature of ecological communities, in particular patterns such as species richness and relative species abundance. Relative species abundance is one of the key features when describing an ecosystem, especially when you are interested in these ecosystems for conservation purposes (Soulé, 1986). It is easy to imagine why; not only are most species rare but rarer species are also more prone to extinction (Hubbell, 2001). UNTB is an elegant theory; it can predict properties of the structure of ecological communities on the basis of relatively simple mathematics and a low amount of assumptions. Such a theory can really teach us a lot about these systems, because it gives us a relatively simple tool with which to generate testable predictions about biodiversity.

The most important difference between UNTB and many other approaches regarding relative species abundance is that it is a more holistic approach. The struggle between holistic and reductionist approaches is a common theme in any kind of science but in ecology especially there has been an emphasis on reductionist approaches for the good latter half of the 20th century (Hubbell, 2001). Reductionist accounts of natural phenomena point to the lower levels of organization as somehow being ontologically more important than higher levels. The lower levels of organization are somehow fundamental and higher levels are merely derived from this. Holism in contrast, is ontologically more plural: different levels of organization all have their own explanatory value which cannot be replaced by simply taking things apart and looking at the parts. There are emergent properties in (biological) systems which are not there if you take only the parts into account. A good analogy might be that a reductionist tries to figure out how a car works by taking it apart and investigating the engine, the wheels and the other parts. A holist tries to understand the workings of the engine and the wheels by looking at how they do their respective jobs in the context of a moving vehicle. For the holist the whole is not only determined by its parts but the parts also by the whole (Looijen, 1998). Though the term holism may have a somewhat mystical connotation, it is important to stress that materialism is not at stake here. Reductionists and holists alike agree, in what Mayr (1982) calls *constitutive reductionism,* that higher levels of organization are made up of lower level entities. Another main difference between holism and reductionism is the direction of causality; For a holist that arrow points down (i.e. lower lever phenomena are caused by higher order phenomena) but for a reductionist it points up (i.e. higher level phenomena are caused by lower level phenomena). Not only are holistic phenomena more complex, they also tend to be less deterministic and more regulated by stochastics. This could be an essential property of higher level processes or just a result of there being more unknown variables. In the latter case the stochasticity would be a property of the model, more than a reflection of reality . This question itself is one that holists and reductionist will most likely disagree on. Either way, a holist theory will often be analyzable in terms of stochasticity (Nelson, 1985) whereas a reductionist theory will give a more deterministic account of the phenomena under analysis.

2.2 The niche-assembly Perspective

With regards to what we can predict about the makeup of ecological communities, there are two traditional approaches to this problem, which appear to be somewhat contradictory: the niche-assembly perspective and the dispersal-assembly perspective. Hubbell describes them as follows:

> The niche-assembly perspective asserts that ecological communities are limited membership assemblages of species that coexist at equilibrium under strict niche partitioning of resources. […] The dispersal-assembly perspective asserts that ecological communities are open, continuously changing, nonequilibrium assemblages of species whose presence, absence, and relative abundance are governed by random speciation and dispersal, ecological drift, and extinction. (Hubbell, 2001 p.29)

The niche-assembly perspective is the more reductionist approach of the two; the composition of an ecosystem in this view is little more than a higher-level summation of processes, which take place on the individual level. The focus on adaptation of individuals leads quite naturally to an equilibrium mode of thinking; because the focus is on adaptation and fitness differences between individuals the step to a view of an ecological community as a collection of niches with a lot of competitive exclusion going on is quickly made.

In essence, the niche-assembly perspective asserts that an ecological community is made up of a limited number of niches, all occupied by a single species. Though there has been no consensus on a full definition for the word “ niche”, a description of the concept does not have to be problematic, if it is kept general. The broadest way to describe a niche is that it is a (hyper-)volume in a set of dimensions which expresses the capability of a species to exploit resources. (Krebs, 2001) These dimensions can be traditional dimensions such as time and space, but they can also represent factors such as prey size, temperature, moisture levels and nutrient availability. The niche of an organism can be seen as the *n*-dimensional space in which a species can live, *n* being the number of factors, which are considered relevant for the survival of the species. Each species will have a *fundamental niche, which* is the *n*-dimensional space in which they can theoretically survive. However, most species will have competitors whose niches may partially or wholly overlap their own. The species which is more efficient in the overlapping part of their fundamental niches will, in a process which is known as niche partitioning or competitive exclusion, exclude the other species by outcompeting them. This can lead to two scenarios; either one species will win and the other will go extinct, or, in a reaction to the evolutionary pressure, one or both species may undergo a change in specialization away from the contested part, effectively reducing the niche-overlap between the two species, thus avoiding extinction. The *realized niche* of a species is the part of their fundamental niche that they actually occupy.

The niche-assembly perspective is widely used throughout ecology, but it has its drawbacks: because of its assumptions about an ecological system having reached equilibrium, the niche-assembly perspective is difficult to apply under certain circumstances: For instance when the environment is very unstable and never reaches equilibrium, such as an area with frequent fires which is often cleared to be recolonized by colonizing species again. It is important to note that a niche-assembly model does not necessarily imply a stable equilibrium state. Yet because the purpose is to explain patterns in biodiversity in terms of differences in niches, the way in which niche-assembly has been used is often one in which it is assumed that a stable equilibrium has been reached. That takes a lot of uncertainty out of the model which would still be there if the equilibrium assumption would not be made.

Other examples of when it is difficult to fully explain the composition of an ecosystem by niche-assembly are environments in which there is no competition for resources and environments that fluctuate so much that competition never leads to extinction before the direction of it is changed again. (Hutchinson, 1959) (Belya and Lancaster, 1999)

2.3 The dispersal-assembly Perspective

The dispersal-assembly perspective works the other way around: It focuses more on large-scale processes, both temporal and spatial. Instead of explaining the composition of an ecosystem in terms of equilibriums determined by competitive differences and niche-partitioning, the dispersal-assembly perspective considers the makeup of an ecological system as dynamic. No longer will the explanation why a certain tree is standing at a particular location be answered with “this particular spot suits his niche the best”. Instead a more large scale, stochastical approach is taken. Factors which are important in determining the current state of a system are for a large part stochastic in nature; Principles such as ecological drift and local extinction are considered to be the key driving factors of ecological systems in this approach. Equilibria are still a key concept in this approach, but their meaning is different from the equilibria used in the niche-assembly perspective. In the niche-assembly perspective an equilibrium means that all species have formed such an assembly that all available niches are partitioned and the composition of the ecological community is thus set in stone, barring invasion by new species or radical changes in the abiotic conditions of the ecosystem. In the perspective of dispersal-assembly an equilibrium merely means that the average number of species on a given island is a function of a set of variables of that island. There is thus an equilibrium in the sense that the amount of species will fluctuate around a certain number but not in the sense that these species will stay he same. In dispersal-assembly theories species are completely exchangeable.

This is best illustrated by MacArthur and Wilson's equilibrium theory of island biogeography (1957). In the equilibrium theory of island biogeography the two key factors that determine where this equilibrium is located are extinction and immigration. If we were to draw an immigration curve relative to the number of species present we would generally expect this curve to be concave and dropping: As more species are present on the island, fewer immigrants belong to new species. At the same time, rapid dispersers would come first and slower dispersers later, meaning that as we go right on the curve the rate of immigration would also drop. Extinction rates, on the other hand, would be concave and rising. More species means more species to possibly go extinct but also, assuming a limited carrying capacity on the island, smaller population sizes per species, increasing the chances of extinction ever further the more we go to the right on the curve. The assumptions leading to the shape of the curves are not trivial; it could be argued that some species might pave the way for other species by changing certain abiotic conditions or that species could benefit from the presence of other species in such a way that the resulting curves might be straight or even convex under certain circumstances. However, I believe these will be special cases and not generally be applicable. For my purposes the exact shape of the curves is not of essential importance.

2.4 Hubbell's perspective

As we have seen, there are two major approaches to answering the main questions about biodiversity and biogeography, the niche-assembly approach and the dispersal-assembly approach. Hubbell claims that "[t]aking the first steps to reconcile these divergent views of ecological nature is the underlying theme of this book" (2001)."

UNTB is not unified to such an extent that it incorporates both the niche-assembly perspective and the dispersal-assembly perspective into one all-encompassing theory. It would in fact be fairer to say that Hubbell presents an extension of the dispersal-assembly perspective on biodiversity. The unification Hubbell has proposed is to start from MacArthur and Wilsons's island biogeography theory and modify it so that it becomes applicable to all kinds of scales, from local, or even individual to global. When discussing larger scales, speciation is added as a factor to the theory of island biogeography. It takes over the role of bringing in new species into the equation, the role that immigration plays on smaller scales.

The UNTB is not meant to be an attack of niche-assemble theory however; Hubbell of course recognizes the existence of niches and their importance in ecosystems. What the question should be is to what extent both niche-assembly and dispersal-assembly play a role in determining the composition of different ecosystems. Both will play a role, but the ratio in which they influence the species-composition within an environment is likely to be very different depending on the environment chosen. This ratio will also depend largely on which species are being inspected; since UNTB assumes neutrality between species, it will likely produce better results in situations where the species are more alike. While UNTB might play a larger role when comparing trees in a closed canopy tropical forest, or other comparable situations with trophically similar species, niche-theory might play a larger role when comparing completely different species.

3. Criticism of UNTB

UNTB has received a fair amount of criticism. The criticism will usually fall in either one of the following categories:

1 - UNTB starts from false assumptions or makes false claims. This argument can either be a direct conceptual attack on the assumptions UNTB makes, or it can come in the shape of the 'empirical test', in which case it is argued that nature fails to live up to the predictions that UNTB makes.

2 - UNTB is not a good theory because it is not reductionist in nature.

In this section I will give an answer to both types of criticisms. I will argue that in the first case the UNTB is turned into a straw man and predictions are falsified that UNTB does not really make. I will argue that this is likely to be because implicitly the second argument plays a role. In the second case I will argue that this reductionist criticism is not valid and I will argue for a holist approach to the neutral – niche debate.

3.1 UNTB starts from false assumptions or makes false claims.

UNTB does start from assumptions that are partly false; there is no big argument here. But many theories describing natural phenomena make unrealistic assumption for reasons of simplicity, elegance and practicality. The most obvious example in the case of UNTB is the assumption of neutrality or selective equivalence between individuals belonging to different species. The question remains however, if this is a proper reason to dismiss neutral theory. By asserting that species are neutral, the UNTB places itself in an interesting position and opens up the possibility for comparison between itself and competing theories. As Friedman has put it:

> Truly important and significant hypotheses will be found to have "assumptions" that are wildly inaccurate descriptive representations of reality, and, in general, the more significant the theory, the more unrealistic the assumptions (in this sense). [...] The reason is simple. A hypothesis is important if it "explains" much by little, that is, if it abstracts the common and crucial elements from the mass of

> complex and detailed circumstances surrounding the phenomena to be explained and permits valid predictions on the basis of them alone (Friedman, 1966)

McGill et al (2006) wrote a critical article against UNTB. Their attack starts with the claim that “[n]eutral theories of biodiversity assert that all individuals of all species are competitively identical. […] This contradicts 100 years of community ecology”. They then continue to use test UNTB against niche-assembly theory and conclude that there is little evidence for UNTB. Dornelas et al (2006) follow a similar approach: They claim that the data they find in coral reefs does not match the predictions made by neutral theory and conclude that “[c]oral reef diversity refutes the neutral theory of biodiversity”.

Though UNTB does assert, for the sake of the theory, that all individuals behave competitively identical, this should not be seen as a weak spot of the theory. UNTB should rather be seen as a theory describing the dynamics of an ecological system assuming there was no such thing as adaptation. The only reason that neutrality is seen as an extra assumption is that competing, more specified models assert that individuals behave in a non-neutral way.

It is thus hardly fair to test neutral theory in this way. Assumptions like “all individuals of different species behave in an ecologically equivalent way” should be seen as leaving out assumptions compared to competing theories, not as adding assumptions. A comparison is to be made with the theory of genetic drift: Examples of evolution by natural selection are not generally seen as proof that genetic drift does not exist. Rather, because genetic drift leaves out a certain set of parameters, it provides a model for the dynamics of genetics in absence of natural selection, and a baseline against which to compare data of cases where natural selection is present.

The situation is the same in the case of UNTB: What happens when the assumption of neutrality is applied is that certain parameters are taken out of the equation. It is thus not an assumption in the traditional sense.

What does it mean then, to “empirically test” neutral theory against niche-assembly theory? If an ecosystem is described of which the mechanics do not match the predictions made by UNTB, this does not mean that UNTB is null and void. Instead it may mean that one of the assumptions of the theory, namely that of neutrality, is, in this case, not valid. If, however, with neutrality applied, the theory can still make accurate predictions about a certain ecosystem, the parameters were apparently not that important, in other words, the assumption of neutrality was probably roughly right. If UNTB fails to deliver good-fitting results, this can be seen as an indication that something else is going on. If niche-assembly theory provides a better fit for a certain ecosystem, this might indicate that in this instance the ecological differences between the measured species play an important role. Instead of claiming that “[c]oral reef diversity refutes the neutral theory of biodiversity”, Dornelas et al. should have claimed something along the lines of: Coral reef diversity is governed by non-neutral principles. Pandolf (2006) phrases his analysis of coral reefs in a more constructive way: "*Ecology: Corals fail a test of neutrality.*" However, it is shown by Volkov et al. (2007) that a neutral model can in fact produce results that fit the observed data well (even though they have make some assumptions that are incorrect).

Instead of criticizing UNTB for starting from false premises, or not producing results exactly matching what we find in practice, we could use it in combination with niche-assembly theory as a very powerful tool to indicate the importance of the ecological differences per ecosystem measured, or per group of species compared. For every ecosystem, the question would be how much extra information the extra parameters concerning non-neutrality add in terms of explanatory power. As a low difference in performance between the two theories is an indication of individuals behaving neutrally and a high difference indicates that there are many ecologically relevant differences between the species, UNTB will effectively work as a null-model for the niche-assembly model. The more UNTB is outperformed by niche-assembly theory, the more important the ecological differences between the sampled species are. This could be measured for instance by performing an analysis of variance. Since different ecosystems differ in the extend to which they are stable or changing we could use a comparison between UNTB and niche-assembly theory over a set of ecosystems to test to what the relation is between stability and the extent to which an ecosystem s niche-governed.

Attacks on UNTB of this type fail to see the role of the theory in a broader context; that of one theory amongst others which can be of practical importance to highlight different aspects of a particular problem that usually go unnoticed or receive less attention than they should. Niche differences have long intrigued biologists, and rightfully so, but they are not the only factor governing the species richness and species abundance distribution in an ecosystem.

In the context of natural selection and genetic drift, the two theories are not generally seen as being mutually exclusive, but rather as two sides of the same coin. In the context of biodiversity and biogeography however, two theories with what is essentially a similar relation are being discussed in a very different way and are not seen as being compatible. The reasons for this difference are elusive but they might be linked to an implicit loyalty to strong reductionist principles, as discussed in the next chapter.

3.2 UNTB is not a reductionist theory.

The other main problem with reconciling the different theories about biodiversity and relative species abundance is that there is a reductionist agenda clouding the discussion. This is not an argument that is often expressed explicitly and precisely because of that it is one that is hard to settle. But the main reason why arguments about testing UNTB against niche theory sound so convincing -and make it into high-profile journals- is that the reductionist story behind these tests is so appealing. It is my claim that, though appealing, the competing-theories way of thinking is counterproductive to getting a full understanding of biodiversity patterns, or in general to how systems work.

There has always been a strong reductionist tendency in the natural sciences and in Biology in particular. There is some merit to this; anything that is solvable with a reductionist approach is relatively easy to oversee. If it is possible to reduce a complex problem to a collection of simpler problems on a smaller scale, the smaller problems can then be solved one by one. They can then be combined to return to the original problem. It is nice to have whatever problem you are working on conveniently arranged this way. This approach does not work for every problem however, and over-applying it could cause us to miss out on emergent patterns that are only clearly observable when looking at the system as a whole.

For instance: there are many disputes between holistic and reductionist approaches in the fields of science that concern themselves with personality, brains and behavior. Properties of persons, such as thinking and experiencing are often held to be incompatible with lower-level properties of neurons, like electrical discharge, that are said to determine these higher-order properties.

In philosophy of mind, this has even become known as the "hard problem". The hard problem consists of there being a seeming contradiction to a physicalist account of the brain an the fact that we have phenomenal consciousness. Different opinions are available on the status of this "explanatory gap". Some philosophers take the explanatory gap as being a proof that physicalism is false (Chalmers, 1995). Others try to denounce our experiences to try and maintain a non dualistic worldview (Churchland, 1981). Neither approach seems very satisfying; following either line of thought means you end up biting the bullet about either physicalism being false (leading towards a dualistic worldview), or to denounce completely patterns and processes which are obviously there.

The problem is that if we follow a strictly reductionist line of thought, if both explanations are true, we have several explanations for essentially the same phenomena and one of them will have to go. This is really a simplistic, black-and-white view of a scientific problem. It is argued by philosophers such as Wittgenstein (1954), Hacker (2003) and Putnam (2000), that trying to solve a seeming discrepancy between several levels of explanation is in fact a misuse of language: exactly because thinking is a property of persons and electrical discharge is a property of neurons, there is no contradiction between saying that a person is thinking or that a neuron is releasing an electrical charge. It depends on the question that we wish to answer which approach is more appropriate.

This also means that certain uses of language must be ruled out; because thinking is a human property and is happening on a certain explanatory level where people and personalities play a role, it is nonsensical to say something like 'my neurons are thinking' or 'I'm discharging my neurons'. It would be weird to intertwine the different levels of explanation in such a way, because it would be like saying; 'my arm is playing tennis'.

In the case of theories regarding biodiversity and relative species abundance, a situation is occurring between the niche-assembly theory and the UNTB which is quite similar (though not identical) to the situation between the neurosciences and folk-psychological accounts of behavior. Niche-assembly is in itself a more reductionist theory than UNTB; it focuses on interactions on the level of individual organisms and from there builds up a picture of the ecological community as a whole. UNTB mainly works top-down: From patterns on a large scale (i.e. the metacommunity and its parameters) patterns on a smaller scale are deduced. On an even higher scale there is the question whether we should try to discern between two seemingly conflicting theories, or try to reconcile them. This is in itself a choice between a reductionist and a holistic approach, which explains why it is no wonder that the former option - conflict – is preferred by those with a background in niche-assembly theory and the latter option is preferred by those with a background in UNTB. Someone who is inclined to a reductionist approach in one area will often have the same preference in another area and similarly for those with a holistic way of thinking.

A scientific account of any system, no matter if it deals with questions about the mind or with ecological systems, should be very clear and consistent in its language use. What is needed is a clear distinction between different explanatory levels, that prevents faulty use of language and thereby prevents false dichotomies. If this were to be implemented in the field of biogeography and biodiversity, the result would be that more research effort could be used to chart the patterns and processes we're so interested in, instead of battling each other over dichotomies that are not, in fact, dichotomies.

The neutral – niche debate could benefit greatly from a broader perspective in which both niche-theory and UNTB play their part. A few properties are essential for this approach to be productive. It would have to see niche-theory and UNTB as supplementary instead of competing theories. The relative explanatory power of the two competing models in different circumstances can be dealt with in two ways. The reductionist approach would imply both sides try to disprove the other theory based on comparing results found with predictions made of both theories. A holist approach would be to incorporate both theories into a broader framework, where the difference in explanatory power of the two models could itself become subject of research and provide the scientific community with exciting new research questions like: "Why are ecosystems of type X more niche-governed than ecosystems of type Y?" or "What is the relation between ecosystem complexity and niche – neutral ratio?" which can improve the predictions we can make about human interference in ecosystems and therefore produce better conservationist practices. I believe the latter option therefore to be the preferable one if we are to succeed in protecting our planet from the various environmental stresses we put it through. Apart from being a reconciliation-orientated approach to the two seemingly conflicting theories, a holist solution would also mean accepting that there is not one ultimate theory governing ecology. Theories should be seen as tools towards understanding patterns and processes, not as dogma's where " there can be only one".

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