The case for ecological neutral theory

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Ecological neutral theory has elicited strong opinions in recent years. Here, we review these opinions and strip away some unfortunate problems with semantics to reveal three major underlying questions. Only one of these relates to neutral theory and the importance of ecological drift, whereas the others involve the link between pattern and process, the tradeoff between simplicity and complexity in modeling, and the role of stochasticity and drift in ecology. We explain how neutral theory cannot be simultaneously used both as a null hypothesis and as an approximation. However, we also show how neutral theory always has a valuable use in one of these two roles, even though the real world is not neutral.

Three key questions that underlie the debate

Understanding of neutral theory has progressed substantially during recent years and the arguments both for and against it have matured. Gone are the days when proponents and opponents of neutral theory could build their cases on good or bad fits of one particular neutral model to some empirical species abundance distribution [1–5]. Here, we complement the recent reviews [6–9] and opinions [10–14] with our own opinion on how neutral theory can aid progress in ecological research. The opposition to neutral theory in ecology is not surprising given its radical assumption and we view such criticism as necessary for neutral theory to grow. The neutral theory of molecular evolution [15] received similar criticism at first, yet it is now accepted as a useful tool. We must reiterate that no one believes the world is really neutral and neutral theory is not a claim that species (or individuals) are ecologically equivalent [16]. Still, we find that these myths persist, and even dominate, at least in informal discussions. Neutral theory is about improving understanding by making some simplifying assumptions about complex systems and seeing what can be explained with the resulting models, a procedure widely accepted in many branches of science that does not require the assumptions to be strictly accurate.

There are many different interpretations of what 'neutral theory' really is (Box 1), and this led both proponents and opponents to 'debate' without being clear what they were debating about. A formal debate requires a well-defined motion and this has been lacking in the discussions so far. We propose the following: 'Neutral theory, an ensemble of different neutral models of community assembly, is useful in ecological research' (Box 1). The usefulness of neutral theory inevitably depends on the context of use. Indeed, even the critics have often 'made use of neutral theory' by producing interesting ecological findings directly through arguing against it [17–19]. Finding data that are unexplained by neutrality [20,21] is a valuable application of neutral theory, not a triumph over it. We feel obliged to discuss semantics here (Box 1), but we do find this a distraction from the main issues.

We identify three key questions that underlie most current arguments about neutral theory: (i) can pattern reveal process; (ii) should simple or complex ecological models be developed; and (iii) is ecological drift a process and is it important? Of these questions, ecological drift is conspicuously the only issue relating directly to neutral theory; the others pertain more to philosophy of science in general and the relative merits of different scientific approaches. We conclude with our case for the utility of neutral theory.

Can pattern reveal process?

In ecology, there is rarely a one-to-one relationship between patterns and processes [22]. The non-spatial species abundance distribution (SAD) in particular does not reveal a unique process [12,23–26], although it can be informative by ruling out models that fail to fit it [27,28], with each model representing a cocktail of processes. This has important implications for neutral theory, which is often fitted to such SADs. Neutral theory shows what a neutral world would look like; unfortunately, many non-neutral models yield similar results according to popular summary data, such as SADs. One example is the broken-stick model [29], which was motivated by the process of partitioning resources into niches. A variety of other models can produce the same SADs

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Box 1. The semantics of neutral theory

The term 'neutral theory' is widely (but regrettably) used in ecology to mean different things, leading to misconceptions that take the debates in a less fruitful direction. For some, the term is used purely interchangeably with 'null model'; to others it refers specifically to the contents of Hubbell's book [1]. We use 'neutral theory' to refer to 'an ensemble of different neutral models by various authors', that retains the spirit of what most think of as neutral theory without having too narrow a scope. If 'neutral theory' were taken instead to be a direct statement that there were really no ecological differences between organisms, then it would be reduced to a straw man; no person supports such a 'neutral theory'. Objections relating to the use of the term 'unified' or 'metacommunity' are again purely semantic arguments, as long as researchers can all accurately communicate, the terminology used should not matter.

Clark argues that neutral theory does not in fact describe true ecological equivalence [10,45] because it is based on the outcome of a stochastic birth–death process and thus species are in fact different, if for no other reason than because they were fortunate in the outcome of stochastic draws. This is also really a semantic argument because, if it were taken literally, one would be forced to label only deterministic models assuming ecological equivalence as 'neutral models' and we agree that such models are unlikely to be interesting. However, there is a clear distinction between models where the probabilities of reproduction and death for an individual depend on its species identity, and models where they do not. It would only add to the confusion if one was forced to invent a new term to distinguish between these two cases. It thus makes most sense to persist with the original definition: neutrality is based on the stochasticity in demographic rates, so fitness equivalence does not mean sameness but equivalence in the probabilistic sense. Furthermore, although the stochasticity in neutral models is likely to be standing in for unknown processes, these might not be rooted in selection; species can suffer in ways that are independent of their species identity. One should be aware of these arguments when interpreting neutral theory, but realize that they are semantic and do not constitute a reason to abandon the theory.

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as those resulting from the broken-stick model [30], including a neutral model with random fission speciation [28].

It is both easy and dangerous to interpret the verbal description that motivates a model as being a fundamental part of the model itself: the same mathematical model and, consequently, its predicted patterns, can often be equally motivated by very different ideas. For example, in the equilibrium theory of island biogeography, MacArthur and Wilson [31] describe a mainland–island model that includes species with different dispersal abilities, but one could replace that description with a neutral interpretation where species have the same dispersal ability and only differ in mainland abundances. The logical rules of the model itself need not change despite this important distinction [32] (J. Rosindell and L.J. Harmon, unpublished manuscript). To further complicate the link between assumptions and processes, the omission of a process from a model is often not stated as an assumption; rather, it is simply outside the scope of the model. In this context, neutrality might not in fact be regarded as an assumption at all [33]; neutral theory can indeed be regarded as having few assumptions rather than many [34]. Different processes (or assumptions) producing the same pattern is a problem, but one that occurs much more generally outside the context of neutral theory; it is simply the problem that pattern does not equal process.

Once one has accepted that pattern does not equal process, it is a small step to accept that individual processes do not affect pattern in a unique way. Consequently, the full complement of individual processes might not be explicitly required to predict patterns accurately with a model. In an analogy, imagine many children each mixing a large number of different colors of paint. One can be fairly certain that each child will mix a similar muddy brown color (one can predict pattern without explicitly modeling process) even though each will do so in a different way (process details do not affect pattern). Although the brown mix does still contain all the colors (patterns are the outcome of many complex processes), it is not possible to tell their proportions just from looking (pattern does not uniquely define process). If one really wishes to know the proportions of colors in the mix (which processes were involved), then one must collect extra data beyond eyeballing the brown color; for instance, dynamically observing the paint-mixing process or looking at multiple patterns (e.g. colors splashed on the child's clothing). Returning to an ecological context, this means that to see differences in the predictions of different models, one needs to consider more data, different types of data and probably dynamic data.

In an ecological context, many of the fundamental patterns of macroecology have been frequently observed in systems outside of ecology [35,36]. This might be interpreted as supporting the idea that process does not affect macroecological patterns in ecology, but one could equally well argue that similar or analogous processes act universally. In this context, the goal of characterizing the importance of fundamental ecological processes is distinct from the goal of predicting and understanding macroecological patterns.

Should simple or complex ecological models be developed?

More than four decades ago, Levins [37] pointed out the inevitable tradeoff between generality, precision and realism of mathematical models in population biology. Although models involving extra processes or exploiting extra information need not be very complex, there is no doubt that every extra process added to a model does have a cost, in terms of understanding the model, its generality and the ability to test its predictions. In the extreme case, an impossibly complex beast is created, and little more can be understood about it than about the real world itself. There will always be a need for models at a variety of stages of the complexity scale, but the cost of increasing complexity is in general underappreciated. The development of computers has enabled the study of extremely complex models in recent years, but it is tempting to exploit the technology to add too much complexity at the expense of generality, predictability and understanding. We suggest that one should understand the simpler model and its limitations before progressing to more complex models. When simple models, such as neutral models, fail, they do so in informative ways because of something that was left out and that can often then be identified. This is in contrast to a more complex model that, if it can be tested at all, might also fail because of components it erroneously included. One should start with ecological questions and then think carefully about what level of complexity is needed to answer them.

The simplicity and tractability of many neutral models is a great asset to neutral theory, but that alone does not constitute a reason to value the theory. A good theory need not be simple, but given several theories that explain the same phenomena equally well, the simplest is the preferred (Occam's razor) [38]. If a cell biologist proposed an intricate cell-based explanation for all ecology, we ecologists would not immediately comply and start thinking at the cell level for all our research; the cell biologist would be expected to show that those more complex (once scaled to the community level) explanations do more for us than the simpler ecological framework. Similarly, neutral theory says that one does not need to invoke different niches or habitat types to explain some patterns. The burden of proof lies with those advocating more intricate explanations for phenomena to show that they explain more by doing so. We expect this to mean investigating other types of data, such as evolutionary and dynamic data, and should ultimately leave only parsimonious (possibly non-neutral) explanations for new and interesting patterns.

Is ecological drift a process and is it important?

Ecological drift refers to the random fluctuations in population size that result from ecological equivalence in the probabilistic sense: individuals have equal chances of reproduction or death regardless of their species identity (Box 1). In a recent unifying framework, drift was named as one of the four key processes in ecology, the others being speciation, selection and dispersal [11]. Neutral models encompass any combination of these that excludes selection.

Clark [10] argues that the stochastic components in models, including ecological drift, represent noise or an error term describing what is not yet understood about a system. He argues that one should aim to convert these 'unknown' (stochastic) components of models into 'known' (deterministic) components. In this context, ecological drift appears to be an unsatisfactory 'explanation' for anything because it is not regarded as a real process but rather is merely standing in for deterministic processes acting at a finer scale.

We feel that research goals should not always be to 'explain' stochasticity with determinism. Apart from being impractical, pursuing this goal can only make models more complex and is at odds with the need for simple models as well as complex ones. The goal of simplifying existing models (possibly by using stochasticity) is equally valid. Furthermore, complex deterministic models can yield chaotic behavior that appears random and, conversely, stochastic systems can have deterministic components; for example, their expected behavior is deterministic. Stochasticity in a model is much more than the 'unexplained' component: stochastic processes encompass knowledge in their distributions. For example, a dispersal kernel contains valuable information [39] about the chance of a dispersing seed reaching certain distances from its origin; however, it must be stochastic because the deterministic alternative is impractical. In the case of ecological drift, Ricklefs [14] suggests that 'deterministic influences of specialized pathogens' are the cause of patterns resembling those arising from stochastic neutral theory. We

agree with the essential idea that neutral drift can result from deterministic processes that are complex and not well understood. In this context, two distinct research goals emerge: first, to use neutral models to approximate and predict these apparently neutral processes in the most parsimonious way possible and, second, to develop more specific fine-scale models involving factors, such as the specialized parasites suggested by Ricklefs, to help understand how and why a non-neutral world might appear neutral in some cases.

Ecological drift must be caused by something at a lower level, but it could still be thought of as a process at a higher explanatory level. When asking whether drift constitutes a 'process', one must be aware that the answer is influenced strongly by perspective. The world appears to be arranged in a hierarchy of different levels of detail and, consequently, so is science. Those interested in processes at a high level usually find processes lower down on the hierarchy irrelevant because of the dominance of emergent properties at higher levels. Conversely, those interested in lower-level phenomena find higher-level processes 'process free'. Whether the real world is, in the strictest sense, fundamentally stochastic or deterministic is another interesting question, but is outside the scope of this article. What is important is how to interpret stochasticity in models and how best to model elements that may be unknown but intractably complex, outside the scope of interest, or acting on a different scale.

A key question is how strongly ecological drift contributes to community assembly. Neutral theory has not only heightened awareness for drift [1], but also shows that it is difficult to quantify drift versus selection merely by studying community summary data, and detailed experiments are often required. For example, Seipielski *et al.* [40] conducted manipulative experiments and were able to show that two *Enallagma* damselfly species do indeed appear to be ecologically equivalent. They argue more generally for a layered view of community structure that integrates both niche and neutral ideas. We agree that ideas from niche theory and neutral theory should be integrated, but we also argue that neutral theory remains useful on its own.

The utility of neutral theory

As null model or an approximation but not both

The predicted abundance distribution of neutral theory is very robust, even to the breaking of neutrality [41–43] and of other assumptions [16,44]. Some have used this to argue that neutral theory is not useful as a null model because it gives the same results as niche models and, thus, cannot detect neutrality [10,45]. However, this argument is essentially just a restatement of the pattern–process problem and is specific to certain data types. If data cannot tell two models apart based on sound statistical methodology, then there is an insufficiency in the data. The models detect the problem but do not cause it. To solve the problem, more and different types of information are needed. Models incapable of making predictions beyond those used for testing restricted data can be criticized on these grounds, but neutral theory makes many testable predictions beyond the non-spatial SAD that receive little or no attention [7,8].

For example, it can predict beta diversity [46], spatial structure [47], species–area curves [48,49], population and community dynamics [50,51], phylogenetic tree shape and branch lengths [52,53], endemicity of species on islands [54] and much more [7,8]. In our opinion, future work should do more to test these patterns. We do not expect the equivalence of niche and neutral models [42] to hold true against all further tests. For example, the spatial patterns of a pure niche structure can be different from those caused by pure dispersal limitation, but appear the same (as in [42]) when everything is well mixed in space. Niche theory as a whole might make more predictions than neutral theory [55], but in this context 'niche theory' refers to almost all ecological models that are not neutral. Similar to all theory, neutral theory does have a scope and some predictions simply fall outside this.

As argued by Gotelli and McGill [56], if neutral models are being used as null models, then an alternative hypothesis must be stated. The appropriateness of neutral theory as a null will thus depend on the hypothesis that it is a null for. One new possibility is to regard neutral models as null models, not for the actual existence of niches, but rather for the detectability of niches in different empirical data sets. Of course data collected for the explicit purpose of finding niches will succeed in that goal, but niches might not be detectable in more general summary data. If neutral theory fits a particular data set, it does not replace existing explanations for those data, but it should cause scrutiny of the current explanations that are sufficient, but not necessary to explain the data. Neutral theory as a null model does not provide the solution to the problems it uncovers in this capacity, but the same is true of any null model.

The argument that neutrality is not useful as a null model, because it makes predictions that are essentially the same as those emerging from non-neutral theory, implies conceding that the non-neutral explanations are not necessary to make accurate predictions. It follows logically that neutrality must be useful as an approximation and its significant tractability advantages over the alternatives should make it extremely powerful in this role. Conversely, stating that neutral theory is not a good approximation implies arguing that it fails to fit data and, hence, in failing the model, yields useful information as a null model. If neutral theory never succeeded in fitting any data, then its use would of course be diminished, but we already know this is not the case. We expect that, for some macroecological data, neutral models will prove useful as an approximation; for other types of data, they will prove useful as a null model. Neutral theory cannot be useful in both capacities simultaneously because being useful as an approximation requires it to succeed in its predictions, whereas being useful as a null model requires it to fail (at least some of the time). In Box 2, we give some examples where neutral theory has served ecology in these roles by failing (or succeeding) to fit various data sets.

In conservation

It is appealing to say that conservation decisions should be made from a perspective of full knowledge of all species and processes going on in a system [10]. However, such full knowledge or the ability to use it tractably in models is far

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Box 2. Examples of the use of neutral theory

In the main text, we discussed several possible uses of neutral theory. In particular, we focused on how neutral models have a utility in cases where they succeed in fitting data and in cases where they fail. Here, we illustrate this with some examples.

Although neutral theory with a basic spatial structure consisting of a well-mixed metacommunity and a separate local community can fit species abundances in a single forest plot, it cannot simultaneously fit species abundances in three distinct forest plots with the same parameters as obtained for a single plot [71]. This highlights a role not only of niche differentiation, but also of spatial structure that the spatially implicit model misses.

A spatially explicit neutral model that respects the network structure of a river and its tributaries captures the species richness of riverine fish very accurately. This implicates a key role of dispersal and the spatial structure of the river network in explaining riverine biodiversity [34].

A neutral model fails to explain the increase in abundance of some tree species for the amount of time they have been present: they increased their abundance faster than chance allowed and thus are expected to have had a competitive advantage of some type [6,7,51].

A neutral model provides a quantitative baseline against which the pace of change in ancient communities, as indicated by fossil data, can be compared [72]. In this capacity, neutral theory showed that over timescales larger than 3000 years, the pace at which communities changed was slower than expected from a neutral benchmark.

A neutral model provided the first mechanistic explanation for the full S-shaped species–area relationship with three phases, the second of which follows the classic power law [48]. It also showed the importance of long-distance dispersal in the system because without this, the gradient of the most frequently observed second phase was too shallow on logarithmic space [59,73]. Furthermore, long-distance dispersal events can stand in for speciation in this model [49], which might be true much more generally.

Neutral theory and its failures to explain the mean lifetimes of species [69] have given rise to the concept of protracted speciation [17]: a simple speciation model that includes the concept that speciation is a gradual process. This concept was later used in the birth–death model of diversification, where it provided a new explanation for observed slowdowns in diversification rates [74].

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from being a reality. Stochasticity can be very helpful for predicting the survival of species [57]. Much work on the conservation biology of entire areas has emerged from simply extrapolating a power law species–area curve [58]. This practice has been criticized for missing many important factors [59] and for being mathematically incorrect [60], but one point that even the critics acknowledge [59] is that species–area relationship extrapolation has the advantage of not needing to have species-specific details, about which unfortunately so little is known. Neutral theory has the same advantage while potentially including more biological details than the extrapolation of simple species–area relationship extrapolation. We consequently expect versions of neutral theory to be useful as tools in some conservation applications although we do, of course, caution for neutral models to be used and interpreted alongside the results from other methods.

As a foundation for other models

Neutral theory is useful as a foundation or motivation for other models. For example, it has been used as a starting point or inspiration for more complex non-neutral models. An important example is the development of nearly neutral theory in ecology [61–63], and work calling for, or

attempting, a unification of niche and neutrality [24,42,43,55,64–67]. Purves and Turnbull [13] argue that a mechanism to maintain precisely equal fitness between individuals (neutrality) over long periods is very difficult to envisage. Both selection and ecological drift are indeed at play in most ecosystems; so further development of nearly neutral models is needed.

As a tool for integrating ecology and evolution

A further possible use of neutral theory is to approximate macroevolutionary patterns and, in doing so, perhaps help to unite ecology and evolution, which is a key goal of modern biology [68]. However, a purely neutral model demonstrates slow dynamics compared with those observed in the natural world [18,19,69] and thus makes unrealistic predictions about timescales; for example, when applied to phylogenetic trees [52]. Environmental stochasticity provides a possible neutral solution [70]; alternatively nearly neutral models [61] might help. Neutral models might still be successful at describing macroecology without invoking macroevolution; for instance, if deep time has little effect (or a fast decaying effect) on present-day macroecological summary data. This area needs further investigation with testing against empirical data. We agree that deep-time evolutionary predictions are a significant problem for neutral theory as it stands, but this is an interesting finding in its own right and it does not yet represent an insurmountable problem or a cause to abandon the theory and its other predictions.

Concluding remarks

Ecological inquiry is sufficiently diverse that researchers will continue to need a multiplicity of approaches and models [37]. Neutral theory must ultimately fall into place as part of the spectrum of different tools that are available. To achieve this will require moving beyond semantics, with each position being clearly defined. Neutral theorists must acknowledge the limitations of the theory and opponents must acknowledge its uses. The time has now come to move forward and embrace the neutral theory of ecology as one of several tools that help advance understanding of biodiversity. A concerted effort should be made to integrate the ideas of both the proponents and opponents to converge on new concepts that draw from the foundations laid down by classic neutral theory and niche theory alike.

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