

Neutral and Niche Theory in Community Ecology: A Framework for Comparing Model Realism

Katie H. Morrow

Universität Bielefeld, Philosophy Department

katherine.morrow@uni-bielefeld.de

Abstract

Ecological neutral theory has been controversial as an alternative to niche theory for explaining community structure. Neutral theory, which explains community structure in terms of ecological drift, is frequently charged with being unrealistic, but commentators have usually not provided an account of theory or model realism. In this paper, I propose a framework for comparing the “realism” or accuracy of alternative theories within a domain with respect to the extent to which the theories abstract and idealize. Using this framework I argue, contrary to most previous commentators, that neutral and niche theories are similarly realistic. Realism cannot provide a basis for accepting or rejecting either type of theory; instead, community ecologists should continue working with a plurality of models. While theoretical unification may become possible, we should treat a plurality of complementary, partial models as the expected situation within community ecology.

Keywords: Ecological drift, ecological equivalence, Hubbell, modelling, abstraction, idealization

1. Introduction

There are two major strategies for explaining the structure of ecological communities.¹ Traditional explanations of community structure appeal to the niche and niche-related processes such as resource partitioning and interspecific competition. The second strategy—a more recent and controversial theoretical development—is to explain community structure by appeal to neutral dynamics. The most influential neutral theory and my focus in this paper is Stephen Hubbell’s Unified Neutral Theory of Biodiversity and Biogeography (UNTB), published as a book in 2001. Neutral theories appeal to events such as birth, death, and migration, which are assumed to occur with equal probability for

¹ Ecological communities consist of the interacting populations of multiple species inhabiting a given location or type of environment.

organisms of any species, to explain community change. Neutral theories importantly do not represent competitive differences among organisms. Thus, they model community structure as undergoing ecological drift, i.e. fluctuations in population numbers that occur indiscriminately or irrespective of fitness differences.

The neutral framework generated controversy among ecologists. Many found it very surprising that a theory that fails to represent ecological properties of organisms (such as differential use of resources) can accurately reproduce important structural properties of some communities. A lot has been written comparing niche and neutral theories, sometimes with a view to either testing the neutral theory, interpreting its core assumptions, or providing justification for its use (McGill 2003; Chave 2004; Leibold and McPeck 2006; Leigh 2007; Rosindell et al. 2012; Munoz and Huneman 2016). A major concern of many such commentators has been the belief that neutral theory is highly *unrealistic*. For example, ecologists have written papers addressing questions about UNTB such as “why a model whose principal assumption looks so evidently false still deserves consideration” (Chave 2004).²

As suggested by these comments, some community ecologists are concerned about theory or model realism, meaning roughly representational accuracy. The literature on theory realism in ecology is strongly influenced by Richard Levins’ classic argument that realism trades off with other properties of a theory such as generality (Levins 1966; Levins 1993; also Orzack and Sober 1993; Odenbaugh 2003; Weisberg 2006; Elliott-Graves 2018). A

² In this context, “theory” and “model” are used interchangeably. The “evidently false” assumption referenced in the quote is the assumption of ecological equivalence, which I discuss in Section 6.

recognized problem within this literature is that Levins and others sometimes use “realism” and related terms unclearly or inconsistently. Thus, there is a need for a clear account of how to assess theory realism in ecology. Such a framework is given by this paper.

It should be noted that I use the term “realism” in this paper only in the modelling sense. I take this model property to be distinct from and likely orthogonal to the issues in the core scientific realism literature, e.g. issues about truth and reference. To illustrate, it could be that a model’s terms refer to “real” objects, yet the model is highly idealized and therefore fails to be an accurate (model-realistic) representation of a system. Or, it could be that a phenomenological model very accurately (model-realistically) captures the dynamics of a system, yet does not contain terms referring to many “real” components of the system. In what follows, I will use “real” and “realistic” only in the modelling sense.

In this paper I propose to evaluate realism in this sense with respect to abstraction and idealization. Abstraction is leaving out detail from a theory, while idealization involves distortion of a representation relative to its target (Jones 2005; Godfrey-Smith 2009; Elliott-Graves and Weisberg 2014; Levy 2018). I will compare niche and neutral theories with respect to how they abstract and idealize in order to argue that they are similarly realistic theories (or similarly unrealistic, depending on one’s perspective). In my discussion, I respond to several authors who claim that niche theory is more realistic, and I also respond to Jay Odenbaugh (forthcoming) who argues that UNTB is more realistic.

My argument has several implications for ecological theorizing and for philosophical views about model pluralism and unification. A direct upshot is that realism cannot be used to choose between these theories. Instead, my analysis suggests that community ecologists ought to continue working with a plurality of theories in order to represent different facets of

communities. Niche and neutral theories should be seen as complementary rather than as competing frameworks (or research programs: see Bausman 2019). Although theoretical unification may ultimately be possible, the persistence of multiple complementary models should be treated as the expected outcome, not as a failure. I further explore these themes at the end of the paper.

The discussion is organized as follows. In section 2 I propose a framework for assessing theory realism based on how theories abstract and idealize. In sections 3 and 4, I present niche and neutral theories, respectively, in more detail. In sections 5 and 6, I evaluate niche and neutral theories for realism using my framework. I argue they are similarly realistic theories. Finally, I conclude with a discussion of the implications of my argument for thinking about pluralism and unification in community ecology.

2. Framework for Assessing Theory Realism

In this section I develop a framework for assessing the realism of ecological theories. The literature about UNTB and realism focuses on the theory's putatively false assumptions and its omission of certain ecological properties of species. The focus on what is omitted from UNTB suggests that it is appropriate to interpret the discussion of theory realism in terms of abstraction and idealization.

Abstraction and idealization are central to modeling practice and both involve leaving stuff out from models. Specifically, abstraction is omitting detail from models, while idealization involves deliberately distorting or fictionalizing a model relative to a target system, often though not necessarily in a way that simplifies the model (Jones 2005; Godfrey-Smith 2009; Levy 2018). Thus, leaving out the atmosphere from a model of the earth is an abstraction, while modelling the earth as a perfect sphere is an idealization. In this section I

will show how abstraction and idealization relate to realism. In the remainder of the paper, I will utilize the concepts of abstraction and idealization to refine our understanding of UNTB and to assess claims about its realism.

Everyone should agree that highly idealized models are less realistic representations compared to less idealized models of the same phenomena, all else being equal (Wimsatt 2007; Godfrey-Smith 2009; Potochnik 2017; Levy 2018). This is because idealization, by definition, involves the distortion of a model relative to its target. While philosophers have recognized the connection between idealization and realism, this connection has not frequently been exploited for evaluating biological theories such as UNTB.

The relationship between abstraction and realism is more complex. There are a few ways one might approach this relationship. First, one might think that leaving out certain details from a model does not affect or even improves the representational accuracy of a model. This is the approach of Jay Odenbaugh (forthcoming) and of Michael Strevens (2004). These philosophers emphasize the representational value of eliminating explanatorily irrelevant variables from proposed models or explanations. The idea is that models that abstract away from extraneous detail will be more faithful representations of which core processes explain a phenomenon.

A contrasting position is the view that a model that is highly abstracted compared to another model is less realistic. On this view, realistic models must capture a certain degree of detail—perhaps causal or mechanistic detail—about the structure of a system. This perspective is held by many ecologists, for example: “In ecology there is also a preference for specific, typically small-scale and detailed models, perhaps because these are more practical to construct in a way that is satisfactory from a *realist* perspective” (Wennekes et

al. 2012, 260, emphasis added). According to these ecologists, they tend to view detailed models as both more realistic and more desirable.

The two presented viewpoints on the relationship between abstraction and realism need not be in conflict; rather, they represent the distinct emphases of different authors. That is, the cited philosophers focus on the problem of eliminating irrelevant factors, while some ecologists focus on the challenge of including enough ecological detail in models. These goals are not mutually exclusive. For the purpose of evaluating ecological theories, I will take the position that abstraction relates to realism in the following way: realistic models balance the two factors just cited. Thus, a realistic model achieves a balance between (A) representing a target system with adequate detail while (B) omitting details that are not explanatorily relevant to a target.

How much detail counts as adequate will depend on many situational factors, including disciplinary norms, as well as empirical facts about how many factors are explanatorily relevant to a target phenomenon. It is also likely not possible to assign an absolute degree of realism to a model. So, I assume that assessments will always be made comparatively. As in the case of community ecology, if we have a pair of theoretical frameworks applied to a given domain, we can compare the extent to which they idealize, and how they balance the abstraction desiderata (A) and (B). In some cases, models will be too dissimilar to be usefully compared along these dimensions. However, I will show that relatively straightforward comparison is possible between neutral and niche theories.

With respect to abstraction, different commentators on UNTB have implicitly stressed either (A) or (B). Thus, some ecologists have argued that UNTB is less realistic than niche theory because UNTB is putatively more highly abstracted, i.e., they claim it does not

represent systems with adequate detail as per condition (A). In contrast, Jay Odenbaugh has argued that UNTB is more realistic than niche theory, because he thinks that niche theory includes non-explanatory details, i.e., it fails on condition (B). I will argue against both of these claims. Both UNTB and niche theory satisfy conditions (A) and (B) similarly well (or similarly poorly). So, I conclude that UNTB and niche theory are similarly realistic.

In what follows, I will give a more detailed overview of the theories, and then I will evaluate them with respect to abstraction and idealization.

3. Niche Theory

I begin with niche theory, since it has historical precedence. Loosely speaking, a species' niche is its place or role within an ecological community. The niche has been conceived slightly differently by ecological theorists over time, but remains an explanatorily central concept.³ For the purpose of this discussion I focus on *resource* conceptions of the niche: a species' niche is the sum of resources it utilizes or requires (Hutchinson 1957; Griesemer 1992).

In ecological theory, the way niche space, or available resources, are allocated among species is thought to be a key driver of community assembly. Niche theorists expect that the way species differently utilize resources should drive different patterns of abundance. For example, a species that utilizes an abundant food resource is expected to be more abundant

³ For example, Grinnell (1917) describes the niche in terms of habitat needs; Elton (1927) describes the niche in terms of trophic functional roles; Chase and Leibold (2003) describe the niche in terms of reciprocal interactions between the species and its environment. These conceptual developments do not make a difference at the level of this paper's discussion.

(all else being equal) than a species that utilizes a scarce food resource. Species that require similar resources are expected to be under intense competition, which will affect their relative abundances. Thus niche phenomena are thought to explain various community level patterns such as why certain species can or cannot coexist; the geographic ranges of species; and properties of communities pertaining to the relative abundances of species.

While all niche models share this general perspective, there is not a single “niche theory.” Rather, “niche theory” refers in the collective to any niche- or competition-based models of communities.⁴ The feature that these otherwise heterogeneous models share is the assumption that species-specific properties drive community dynamics.

Here I will make a brief digression to address a concern raised by some philosophers about the niche concept. James Justus has argued that the niche concept is too heterogeneous, disunified, and unclear; and that it does not play a central role in actual competition-based models of communities. So he thinks the niche concept is problematic (Justus 2019). I don’t agree with Justus’ position, but arguing for this is beyond the scope of this paper. If you share Justus’ concerns, you can read my discussion about niche models throughout this paper as referring to competition-based models. Because my main aim in this paper is to compare two modelling approaches, rather than to reconstruct the concepts underlying the models, it should not make a difference to my argument whether you accept the niche concept. I will continue to use the standard terminology of referring to competition-based and resource partitioning models collectively as “niche models.”

⁴ “Niche theory” might be read in an even broader sense, to mean all ecological thought related to the niche. For the purpose of this paper, I restrict my discussion to niche-related models of communities.

An influential principle derived from niche or competition theorizing is the principle of competitive exclusion, which states that species with the same (realized) niche cannot coexist indefinitely.⁵ Relatedly, the evolution of niche differentiation is taken to explain why otherwise similar species, such as different species of related songbirds, can coexist in the same region.

A challenge for niche theorists has been whether the core prediction of competitive exclusion holds up across ecological systems. If competitive exclusion fails to occur in some systems, this would suggest that niche-theoretic explanations fail to capture all the processes that drive community structure. This is relevant to our assessment of theory realism since it pertains to the inclusion or omission of explanatory factors.

The empirical evidence for competitive exclusion has been mixed, a fact that has motivated the development of alternative neutral models. Evidence in favor of competitive exclusion has been obtained from a limited number of systems that are relatively simple to experiment on. A classic source is the experimental work done by G. F. Gause on *Paramecium* and *Styloynchia*, during which one species always displaced the other over time in laboratory flasks (Gause 1934). A case often cited in contemporary textbooks is that of two species of acorn barnacle, where one species was shown to restrict the realized range of the second species to the upper part of the intertidal zone due to the former's superior competitive ability in the rest of the intertidal zone (Connell 1961a; Connell 1961b). This case was ideal for study due to the easy experimental manipulability of sessile barnacles.

However, there are other cases that are prima facie counterexamples to the principle of competitive exclusion. The classic discussion of this is G. E. Hutchinson's (1961) "The

⁵ An important early statement of this principle is due to G. F. Gause (1934).

Paradox of the Plankton,” in which he describes the apparent violation of competitive exclusion by the huge numbers of ecologically similar phytoplankton species that simultaneously occupy large bodies of water.⁶ A more recently discussed case involves two genera of North American damselfly. These damselfly genera, *Ischnura* and *Enallagma*, exhibit a trade-off between growth and predation risk at the genus level. More specifically, *Ischnura* grow more efficiently but *Enallagma* better avoid predators (Leibold and McPeck 2006). This is at first glance the sort of ecological differentiation that is predicted under niche theory. However, the species within each genus are extremely biologically similar (aside from their reproductive isolation), and multiple species within each genus can occupy a given lake at the same time. The authors propose that “each genus [could] essentially operate as a separate functional group within the food web, with the ecological dynamics of the food web regulating the total number of *Ischnura* and *Enallagma* individuals, respectively, and not the abundances of each species separately” (Leibold and McPeck 2006, 1405). In their view, the species within each genus fail to exhibit ecological differentiation, contrary to the prediction of the competitive exclusion principle. It would be difficult to overstate how surprising this case looks from the perspective of traditional niche-related thought.

Further research will no doubt continue to contribute to the understanding of how often competitive exclusion holds in nature. However, conducting experiments within real communities to investigate this has been challenging. One problem is that while one can directly manipulate the species present in a community, it is more difficult to directly manipulate the occurrence of a process such as competition. A second challenge is that

⁶ Hutchinson does propose a niche-theoretic solution to the apparent problem in the paper, although I’m unsure whether the solution should be considered adequate.

different theoretical explanations (e.g., competition versus drift) can predict similar outcomes. Thus, in some cases in which the predicted outcome of competitive exclusion appears to have occurred, the outcome could be explained by a process other than competition. This makes it difficult to discriminate between processes on the basis of observational data, a well-known challenge among community ecologists. A third challenge has to do with providing sufficient evidence for the absence of a process. A committed niche theorist might feel that they have adequate theoretical justification for believing that competitive exclusion always occurs, so there must be some ecological differentiation not yet discovered among species in cases that are apparent violations of the principle. Thus, there is a general evidentiary question about how to show that a certain process is *not* responsible for a given outcome.

Consider the second challenge in more detail. For a majority of studied communities, we only have data about community patterns or outcomes. To illustrate, we might observe that ecologically similar species fail to occupy the same islands in an island chain. This observation, while compatible with the past occurrence of competition, does not entail that competition produced the outcome. For example, the pattern could be explained by historical dispersal routes rather than by a competitive process. As a result, observing the pattern fails to either confirm or disconfirm a niche-based explanation. The ecologists working on contemporary community theory have appreciated the importance of this problem, which might be described as the *underdetermination of processes by patterns* (my phrase, but see Du et al. 2011; Rosindell et al. 2012). In light of this underdetermination, some ecologists have investigated whether alternative models can predict observed patterns as well as traditional niche models.

To summarize, some communities have structures that appear to violate key expectations of niche theory, and it is often difficult to obtain direct evidence that competition is responsible for shaping community structure. Thus, there is reason to suspect that niche theory may exclude some important processes generating the structures of some communities. Among other considerations, these have motivated the development of neutral theories in ecology, which attempt to explain community structure without reference to niche-based processes. I turn to an important neutral theory in the next section.

4. Ecological Neutral Theory

In the 1990s, some ecologists departed from the niche tradition and proposed neutral models of community assembly. These models treat biodiversity patterns as outcomes of stochastic and *neutral* (i.e., indiscriminate or fitness-indifferent) processes rather than of competition. In these models, species-specific differences among organisms are treated as irrelevant to community dynamics. The most influential such work, and the one I will focus on in this paper, is Stephen Hubbell's (2001) Unified Neutral Theory of Biodiversity and Biogeography (UNTB).

Hubbell's theory is a mathematical framework for predicting community and metacommunity composition. Note that in UNTB, different trophic levels must be treated separately, so the communities picked out for the purpose of this theory consist of organisms within a single trophic level.⁷ Examples of trophic levels are primary producers (e.g., plants)

⁷ A reason for this restriction is that UNTB treats communities as saturated with individuals, such that one individual being in a given spot excludes any other individual. This makes sense as an approximation for the behavior of trophically similar organisms (e.g., trees), but

and herbivores. Traditional niche theorists would expect there to be a great deal of niche differentiation within a trophic level. The surprising feature of UNTB is that it does not represent any of this niche differentiation.

UNTB represents communities in the following manner. First, communities are modeled as a saturated grid of individuals. The theory makes a zero-sum assumption that one individual must die in order for a new individual to enter the community. Individuals can enter a community by migration (from the surrounding metacommunity) or via reproduction of nearby organisms. Second, the diversity structure of a community (e.g., the relative abundances of species) is treated as resulting solely from individual-level events. The possible events in UNTB are death, reproduction, dispersal, and speciation. In UNTB, speciation consists simply of an individual leaving an offspring with a new species identity. Speciation must be included in the model in order to replace species that go extinct, which occurs when all of a species' members die without reproducing. UNTB attaches a probability of each of these events to each individual, with the result that the community undergoes stochastic drift over time. The third and most important feature of UNTB is that it treats organisms of different species within the community as being "ecologically equivalent." Quantitatively, this means that all individuals have equal probabilities of undergoing events like death and reproduction. Biologically, this means that UNTB treats species membership or species-specific properties as conferring no competitive advantage or disadvantage to organisms. The speciation rate in UNTB will influence the species richness predicted by the

not for trophically dissimilar organisms like a tree and a bird that do not occupy the same physical spaces in a forest. Restriction to a trophic level is not unusual—many ecological studies and models focus on a single trophic level.

model, but species identity confers no advantage to an individual. The controversial feature of UNTB is that all features of community structure are explained within this neutral framework that ignores competitive differences among organisms.⁸ This is a major way in which it departs from niche models.

UNTB has generated controversy since it was first developed. Ecologists were initially surprised by how well this theory can predict structural features of some communities. The theory has generated controversy because many ecologists have claimed that it is less realistic than niche theory because it leaves out ecological differences among species. Some ecologists view realism as a key theoretic virtue, and based on this they prefer niche models over neutral theory (see Wennekes et al. 2012). In the following sections I look more closely at UNTB to see whether this claim about realism is warranted. I will argue that neither UNTB nor niche theory has a clear advantage with respect to realism.

5. Abstraction

First I will show that UNTB and niche theory are similarly realistic with respect to the detail they include and omit. Recall that there are two ways abstraction hooks up to realism:

- (A) Realistic theories represent a system with adequate detail to explain the target phenomena.

⁸ There is some analogy to evolutionary drift, but a close parallel with evolutionary theory should not be assumed. Hubbell developed UNTB primarily as an extension of another neutral ecological theory, the Theory of Island Biogeography (MacArthur and Wilson 1967).

(B) Realistic theories omit details that are not explanatorily relevant to the target phenomena.

My conclusion will be that often, both drift and competition contribute to explaining ecological community structure.⁹ Because traditional niche theories leave out drift, and UNTB leaves out competition, both theories omit a major explanatory factor, while neither includes an irrelevant factor. So, they are similarly realistic (or unrealistic) theories.

Ecologist Paul Wennekes and coauthors view UNTB as less realistic than niche theory in virtue of their view that it is both more abstracted and more idealized than niche theory.¹⁰ First, they claim that UNTB makes false (i.e., idealizing) assumptions. They argue that this makes UNTB less realistic than niche theory, but that the use of UNTB can be justified from a predictive or pragmatic perspective. I will return to this issue about UNTB's main idealizing assumption in the next section. Second, they claim that UNTB is less realistic in part because it omits individual-level detail:

Niche-assembly is in itself a more realist theory than neutral theory; it focuses on detailed interactions between individuals and species and from this 'real' base builds up a picture of the ecological community as a whole. Neutral theory partly works top-down: local community structure is determined, to a

⁹ You might think that some additional processes also importantly influence community properties—for example, evolution. While this paper focuses on drift and competition, it is compatible with my arguments that other processes are also important. UNTB in particular relies on the inclusion of speciation and migration, though both are treated in a highly idealized manner.

¹⁰ Framing this in terms of abstraction and idealization is my interpretation of their argument.

considerable extent, by processes at the metacommunity level. (Wennekes et al. 2012, 266)

Thus, they link individual-level detail with realism; they hold that abstracting from individual details results in a less realistic model.

The cited authors draw a contrast between top-down and bottom-up explanation. Bottom-up explanation contains individual-level causal detail, while top-down explanation abstracts away from this detail and explains a phenomenon in terms of larger-scale processes. While potentially a good distinction, its application to UNTB is misleading. It is true that UNTB can represent larger-scale metacommunity dynamics, while traditional niche theories are limited to local communities. However, this is not because UNTB is a less individual-based or a less mechanistic theory.

UNTB represents (meta-)communities at the level of individual organisms. Community structure is then predicted as an outcome of demographic and dispersal events affecting each of these individuals, e.g. individual trees leaving offspring. This is clearly a mechanistically explicit, individual-level explanation. This is not top-down explanation if “top-down” means that the theory abstracts away from individuals.¹¹ Thus, UNTB illustrates that it is possible for a theory to apply to larger scales but still represent details at the individual level.

In fairness, UNTB abstracts away from most of the properties of individual organisms. UNTB tracks species membership but not the physiological properties of individuals, for instance. However, the same is true of most ecological models, including

¹¹ Also see Levy (2018) for a similar discussion of individual-based population models and abstraction.

niche-based models, which for the sake of tractability leave out idiosyncratic properties of individual organisms. So, there is not any major contrast here.

In addition to considering the inclusion of individual-level detail, we can consider abstraction at the level of processes included in the models. There is a huge number of processes occurring in any given community—nutrient cycling, natural selection, succession, facilitation, circadian rhythms, erosion, etc.—and ecological models must omit most of these and focus on only the most seemingly relevant to given phenomenon. Due to the causal complexity of ecological systems, we can expect ecological models to leave out a lot of potentially relevant processes. This applies equally to niche and neutral theories.

As previously discussed, some philosophers have emphasized that excluding unneeded detail can make a model more realistic. Models that represent too many processes at once suffer from various tractability problems, but what's more important here is that they become less realistic if they fail to pick out those processes that are most relevant to an outcome. From this perspective, Jay Odenbaugh (forthcoming) argues that UNTB is more realistic than niche theory because he argues niche differences fail to be explanatory of community structure. I will summarize and respond to this argument.

To support his position, Odenbaugh appeals to an account of causal relevance. This account states that for “a pair of models which differ only with regard to an assumption concerning [whether] a causal factor C is present, takes a non-zero value, etc. C is *causally irrelevant* to our prediction if adding or removing C from our model doesn't alter whether the prediction is implied” (emphasis in original). This test for causal relevance applies to a pair of models that are very similar but differ with respect to the inclusion of a causal factor.

Intuitively, if eliminating a causal factor from a model results in equally good predictions about an outcome, then that extra factor may not be causally relevant to the outcome.

Appealing to this causal relevance framework, Odenbaugh claims that UNTB accurately predicts the relative abundance structure of a community without including niche differences. So, he thinks that niche differences are causally and explanatorily irrelevant to community structure. He concludes that UNTB should be seen as supplying realistic explanations of community structure.

I have several reservations about this argument as applied to neutral theory. There is a background issue about how theories of community assembly should be evaluated. As Odenbaugh also recognizes, testing work needs to bear in mind the distinction between *neutral* theories or models—that explain outcomes in terms of a process of drift—and *null* models—simplified models that are used to statistically test whether a target model supplies a good causal explanation for some data. UNTB is a neutral mechanistic theory of community structure that cannot generally be treated as a null model for the purpose of statistically testing competition-based models. Rather, UNTB itself should be tested against an appropriate null model (Gotelli and McGill 2006; Bausman 2018; Bausman and Halina 2018). Odenbaugh agrees that UNTB should not be treated merely as a null model by ecologists.

However, this raises questions about the comparison procedure proposed by Odenbaugh. The causal relevance framework utilized by Odenbaugh is most informative when a model is designed to be a simplified or null version of another model for the purpose of testing causal structure. When working with two dissimilar types of model, as in the case of neutral versus niche models, comparing predictive accuracy is not a viable way of assessing causal relevance. To illustrate why, consider the well-known fact that highly

simplified, idealized, phenomenological models can sometimes produce excellent predictions, but this cannot be taken to show that few causal factors are at work at a mechanistic level.

A key point is that UNTB is not a simplified niche model. Instead, UNTB and traditional niche models are mathematically and conceptually dissimilar types of model. This means it is not appropriate to test for causal relevance by comparing their predictive accuracy. The predictive accuracy test assumes that models differ only in respect to the inclusion or omission of one causal factor, an assumption violated by many pairs of community models. In such cases, there is no way to eliminate the likelihood that other incidental structural differences between the models partially explain their predictive differences.

A second point is that neither UNTB nor niche models can be privileged as causally simpler in terms of the number of processes included in the model. Neutral models capture drift and, in the case of UNTB, migration and speciation (treated neutrally), while excluding competition or resource partitioning. Traditional niche models capture competition or resource partitioning while excluding drift (and also usually speciation).¹² So, since the model types differ from each other in multiple respects, it is unclear what we should conclude from a comparison of predictive accuracy. A more appropriate comparison would be between a niche model and a structurally similar hybrid model, or between a neutral model and a

¹² Because UNTB includes speciation and traditional niche models don't, you might conclude that UNTB includes more processes and is more realistic. The reason I have not argued for this interpretation is that in UNTB, speciation is not treated in a mechanistically-explicit or realistic manner; it is an instantaneous and fitness-indifferent event. For this reason, it seems ambiguous whether speciation counts towards the theory's representational realism.

structurally similar hybrid model (where a hybrid model represents both niche-related processes and drift). Hybrid models do exist, and if a structurally similar hybrid model made predictions about community structure no better than UNTB, that might constitute evidence that niche mechanisms are not active in a particular context.¹³ My main reservation here is that hybrid models are an even newer development than neutral models, and it seems likely that the predictive accuracy and realism of all model types will continue to improve into the future, making any current comparison seem premature.

My argument assumes that drift can be treated as a process on par with competition. If one assumes that drift results from the *absence* of positive forces or processes, then it is true that UNTB and niche models differ from each other in mainly one respect (setting aside speciation). The latter position is assumed by Odenbaugh's argument (personal communication). Although I cannot here offer a general account of what counts as a process, I will give some reasons for considering ecological drift a *prima facie* process. First, UNTB represents drift in a mechanistically explicit way, as resulting from birth-death-reproduction events. Second, treating drift as the absence of a process may imply that non-neutral processes are automatically explanatorily privileged, but this presupposition could be in tension with empirical facts. Third, interpreting neutral models as representing the absence of niche processes invites the incorrect view that they function merely as null models for competition models. Fourth, biologists tend to use the term "process" liberally, including sometimes referring to drift as a process (e.g., Vellend 2010). (While not decisive, I assume

¹³ Given the complexity of ecological modelling, evidence gained from comparing models' predictive accuracy needs to also be weighed against more direct forms of empirical evidence as obtained by field experimental and observational data.

that the burden of proof should be on philosophers who claim that scientists use terms incorrectly.) Fifth, philosophers have argued persuasively that genetic drift should be treated as a process in the evolutionary context, and I expect that similar arguments can be made in the ecological case (Millstein et al. 2009; though cf. Lange 2013).

Certainly none of these reasons are conclusive, but I believe the burden of proof is on those who would treat drift as the absence of a process for the purpose of evaluating biological models. In addition, given that Odenbaugh's argument relies on a substantive ontological position about the nature of drift, his argument must be considered at least as inconclusive as that ontological position.

I grant that it would be of interest if there were one community model that clearly outperformed all of the others in terms of accurately reproducing diversity patterns across real communities. However, this does not seem to be the way community ecology is heading. Neutral models have been found accurate in tests on some community types (including some tropical rainforests, Hubbell's main system) but not on other community types, where niche or hybrid models perform better (Tang and Zhou 2013). Based on both empirical tests and theoretical considerations, many ecologists now think that communities which are predominately neutral or niche-governed represent ends of a continuum, with many communities importantly influenced by both (Gravel et al. 2006; Chase and Myers 2011). In addition, it is likely that different processes predominate at different spatiotemporal scales. Given this, it would be remarkable if a single model were to emerge in the near future that was clearly predictively superior to existing frameworks across all communities and scales of interest.

UNTB and niche models are all partial treatments of communities that have achieved a level of predictive success. Importantly, there is antecedent experimental and observational evidence that competition is sometimes relevant to structuring communities.¹⁴ Even the most spectacular predictive successes of UNTB cannot be taken to override empirical evidence that competition influences some communities. So, neutral and niche models are not in competition to be the most realistic theory; instead, they are complementary in the sense that they each emphasize an important process. With respect to abstraction, presumably neither of these theories includes irrelevant detail, while each theory omits at least one important process, rendering them both comparably unrealistic according to this criterion.

6. Idealization

As stated earlier, idealization involves distorting a model relative to its target system. Idealization is inversely related to model realism. Many ecologists have thought that UNTB is far more idealized than niche theory. In this section I clarify the nature of UNTB's most prominent idealizing assumption in order to evaluate the extent to which it renders UNTB unrealistic.

The noteworthy assumption is that all organisms are “ecologically equivalent” or lack competitive advantages. Many ecologists have commented on the apparent falsity of the assumption (e.g., Chave 2004; Leigh 2007; Wennekes et al. 2012). Hubbell himself has opined that “the deepest puzzle raised by neutral theory is why it does as well as it does [predictively], despite its radical assumptions,” referring to ecological equivalence (Hubbell 2006, 1387-88). Many ecologists worry that this “radical” idealizing assumption conflicts

¹⁴ See MacArthur (1958) for another classic example.

with commonsense ecological knowledge about species' differences. However, there has been some confusion about how to understand the assumption that has led to premature criticisms of UNTB.

There are several ways in which “ecological equivalence” might be interpreted. I have ordered them from what are intuitively stronger to weaker potential understandings of “equivalence.” This is likely not an exhaustive list, but is illustrative of relevant alternative interpretations.

- (1) All individuals under consideration are functionally identical.
- (2) All individuals under consideration belong to species with the same ecological niche.
- (3) All individuals under consideration have the same probability of demographic and dispersal events.

Among these alternatives, UNTB only requires something like interpretation (3). That is, models of UNTB assign the same probabilities of demographic and dispersal events to all individuals, regardless of species. To clarify, at the population level, different species will have different chances of, say, going extinct by a given time if the populations are of different sizes to begin with. In UNTB, a different chance of going extinct is explained solely by facts about probability and not by any potential difference in competitive ability between species. Thus changes in community composition are treated as being produced entirely by neutral or indiscriminate processes.

Clearly, it is an idealization to treat all individuals (within and between species) in a community as having an equal probability of demographic events. However, in a community

in which different species have a similar average fitness or reproductive rate, this assumption looks more like a warranted simplification and not a major distortion.¹⁵

UNTB does not require assumptions (1) or (2), both of which are more obviously large distortions of biological reality. That is, it is not built into UNTB that communities consist of individuals that are biologically or ecologically identical (e.g., having the same growth strategies, light needs, or mechanisms of pollination). What UNTB does assume is something weaker, for instance, that these differences are irrelevant to the (average) probabilities of demographic events, and therefore not predictively or explanatorily linked to community structure outcomes.

Several authors have thought that UNTB requires assumption (2) that there are no niche differences among species. For example, in their well-known book on niche theory, Chase and Leibold characterize UNTB as “assuming that all species are, in essence, identical in their ecological niches” (Chase and Leibold 2003, viii). Similarly, Gotelli and McGill say that “Neutral models posit that consistent niche differences *are not present* and that community structure can be accounted for by random colonization, migration, and extinction” (Gotelli and McGill 2006, 795, emphasis added).¹⁶ E. G. Leigh, Jr offers the

¹⁵ See Munoz and Huneman (2016) for a more technical discussion of the circumstances under which neutral community behavior can arise—even in communities in which species have fitness differences. A reviewer suggested that there may be some even weaker potential interpretations of the equivalence assumption, for instance that individuals can be *treated* as having equivalent probabilities of events for specific predictive purposes, even in circumstances where competitive differences are known to exist. My aim is to show that interpretations stronger than (3) are not required by UNTB, and this is compatible with the suggestion that even weaker interpretations may be viable.

¹⁶ This is a very helpful article on the challenges for testing neutral models in ecology.

objection that UNTB's "fundamental axiom, that all trees are alike before natural selection regardless of their species, is false," going on to cite examples including the fact that "Different species adjust differently to the master trade-off between growing fast in bright light and surviving in shade" (Leigh 2007, 2081). While I agree with some of the other examples given, Leigh apparently takes the existence of niche differentiation to conflict with the equivalence assumption. I argue that these claims reflect a subtle misreading of UNTB.

One reader suggested that although UNTB only *requires* (3), ecologists might assume that something like (2)—the lack of niche differentiation—is the most plausible explanation for how (3) could hold in a real community. This view could explain the above quotes. While some researchers might believe this, it is false that the lack of niche differentiation is the only plausible way for neutral behavior to arise. It is possible for species to have differences in their niche-related properties and nevertheless to have the same average chance of reproduction. This is because different ecological strategies do not have to lead to fitness differences. To illustrate, imagine two plant species whose flowers are adapted for pollination by different kinds of animal. They may nevertheless have identical expected reproductive rates, assuming both pollinators are abundant enough and the plants' reproductive strategies are otherwise similar. If this is the case, then a community consisting of these two species may be governed by drift, even though the species differ along at least one niche axis. Thus, if ecological differences among species fail to create different average reproductive rates, this will result in neutral behavior of a niche-differentiated community (see Hubbell 2005). Hubbell correctly suggests that UNTB can realistically represent the dynamics of such a community. In this case, contrary to popular belief, the equivalence assumption does not

represent a problematic idealization, and is not inconsistent with the presence of niche differences in a community.¹⁷

Odenbaugh (forthcoming) interprets the equivalence assumption in the same manner: “the neutrality assumption...says interspecific differences *do not make a causal difference* to the patterns of interest and thus are explanatorily irrelevant” (emphasis in original). So, I agree with a conditional version of Odenbaugh’s thesis, namely that UNTB can be considered a realistic representation of a community if that community is in fact primarily undergoing drift, regardless of the presence of niche-related differentiation. UNTB would not be an unduly distorted representation of the assembly of this type of community, because no process with important explanatory relevance to that community’s structure is left out.¹⁸

As Hubbell and other neutral theorists allow, it seems unlikely that the majority of communities are actually fully neutral (i.e., not influenced by competitive differences). The claim that some communities do approximate neutrality is an empirical question that requires experimental evidence (Hubbell 2005; Hubbell 2006; cf. Leigh 2007) as well as better attention to statistical procedures (Gotelli and McGill 2006). However, it is also likely that drift makes a difference in many communities. Thus, the omission of drift from traditional competition models also results in a distorted representation of community behavior. The most realistic model will often be one that includes both drift and niche-related factors.

¹⁷ It’s still an idealization to ignore within-species differences in fitness, but this isn’t the feature of UNTB that has been controversial.

¹⁸ At least, by hypothesis nothing important is left out, but I allow that there may be important factors not commonly included in either model type. Potential examples include evolution, environmental patterns, and effects of within-species individual differences.

Both UNTB and niche models make various idealizing assumptions typical of ecological models in general. These will depend on the exact niche model considered, but such models often ignore within-species differences and omit evolution, for instance. However, the default view is that UNTB is far worse off with respect to idealization, specifically because the equivalence assumption has been taken to be wildly false. This section has argued that the equivalence assumption, interpreted correctly, is not as extreme as it has been portrayed, and may in fact correctly reflect the dynamics of some communities. So, this default view is mistaken.

In short, the gulf in realism between UNTB and niche theory is not as wide as other commentators have thought. UNTB and niche-only models each provide partial representations of community dynamics.

7. Outlooks: Unification and Pluralism

My argument has several implications for future theorizing about communities and for philosophical views about pluralism and unification. As we have seen, appeals to realism have played a prominent role in the rhetoric about UNTB. Based on my argument that neutral and niche theories are similarly realistic, the prior focus on realism has been misleading and will not help with selecting among these theories.

In pursuit of realism, integrated or hybrid theories seem more promising than either niche-only or neutral theories. An important example of an integrated framework is Mark Vellend's theory of community ecology, which proposes that communities are assembled via four processes (selection, drift, dispersal, and speciation) (Vellend 2010; Vellend 2016). These integrated ecological theories should be of interest to philosophers of biology, many

of whom have argued that biology is generally ill-suited to theoretical unification (Beatty 1995; Beatty 1997; Mitchell 2003). However, we cannot assume that such a theory will outcompete existing theories with respect to theoretical virtues other than realism (Levins 1966; Odenbaugh 2005). To illustrate, Vellend's theory has been presented primarily in a qualitative form, much like common statements of the theory of evolution, with the 2016 work containing simple illustrative models. An issue will be whether increasingly inclusive and realistic predictive models remain operable, and whether it will be possible to statistically disentangle the relative contributions of four or more processes at once to real diversity patterns (see Zhou and Ning 2017). In view of these modelling and statistical challenges, the current persistence of multiple, partially realistic theories in community ecology should not be seen as a failure with respect to unification, but rather as a strategy for parsing the complexity of ecological communities.

So, my discussion suggests that unless a single theoretical framework emerges that very clearly outperforms existing ones according to a range of desiderata, we should adopt a pluralistic stance about models in community ecology. Since communities are complex and not fully captured by any major theory or research program, our understanding of communities must be informed by multiple theories that highlight different processes as well as by other sources of knowledge, particularly experimental work (see Longino 2006; Longino 2013).

Some ecologists and philosophers have viewed the state of community ecology as one of "competitive pluralism" (to use a phrase from Sandra Mitchell). On this view, mutually incompatible explanatory strategies are maintained only in response to epistemic uncertainty, and the aim is to ultimately settle on the single best supported theory. In contrast,

I have argued that UNTB and niche models are not in competition, and there is no longer serious uncertainty about the fact that both ecological drift and niche differentiation sometimes operate in communities. So, Mitchell's integrative pluralism model is more apt for this context (Mitchell 2002; Mitchell 2003). On this view we expect there to be multiple coexisting models at the theoretical level, even when there is (in principle) a single integrated explanation for each concrete outcome.

There are additional routes to pluralism. For example, William Bausman has characterized competitionism and neutralism as *research programs* with somewhat different starting questions, key study systems, and methodological approaches (Bausman 2019), and has argued for methodological pluralism within community ecology (Bausman 2022). I largely agree with this position. The present paper focuses on properties of individual models, but reaches a compatible conclusion about pluralism.

There is a question lurking behind my discussion: Why are some community ecologists so concerned about theory realism, and is this concern warranted? There are plenty of cases in which an abstracted or idealized theory performs better for some purpose than a theory with more representational detail. A canned illustration of this is the way subway maps distort the directions and distances between stops in the interest of readability. Examples from science include the way some idealized, higher-level physical theories are better able to explain macro-scale behaviors than micro-scale theories (Batterman 2018) and how the spatial resolution of climate models trades off with the amount of time required to run a simulation, rendering models with too much detail useless (Parker 2014).

Ecologists in community ecology are attempting to develop theories that are highly mechanistically explicit and detailed while at the same time being both general and

predictively accurate. This is surprising given the conventional wisdom that realism (representational detail) trades off with model generality in ecology, partly because of the causal heterogeneity of ecological systems (Elliott-Graves 2018). It is intriguing that community theorists seem to be aiming for both realism and generality at once, as evidenced by the sorts of criticisms and tests levelled against theories of community assembly. It remains to be seen whether it is possible to generate a theory that is simultaneously highly realistic and general, but I have discussed a few of the likely challenges. It could be that community ecologists are holding their theories to impossible standards, and should reconsider the most desirable way to balance desiderata such as realism and generality.

Acknowledgements

Many thanks to Jay Odenbaugh and the anonymous referees for their comments on this paper, and to everyone who had commented on prior drafts of this material, including Colin Allen, Katie Creel, Michael Dietrich, Sandra Mitchell, Rose Novick, Zina Ward, Jennifer Whyte, and Tom Wysocki.

Funding

My research is currently funded by the German Research Foundation (DFG) as part of the SFB TRR 212, “A Novel Synthesis of Individualisation across Behaviour, Ecology and Evolution: Niche Choice, Niche Conformance, Niche Construction (NC³),” project number 316099922.

References

- Batterman RW (2018) Autonomy of Theories: An Explanatory Problem. *Nous* 52(4):858–873. <https://doi.org/10.1111/nous.12191>
- Bausman W (2019) The Aims and Structures of Ecological Research Programs. *Philos Top* 47(1):1–20
- Bausman W, Halina M (2018) Not null enough: pseudo-null hypotheses in community ecology and comparative psychology. *Biol Philos* 33(3–4):30. <https://doi.org/10.1007/s10539-018-9640-4>
- Bausman WC (2018) Modeling: Neutral, Null, and Baseline. *Philos Sci* 85(4):594–616. <https://doi.org/10.1086/699021>
- Bausman WC (2022) The Role of Starting Points to Order Investigation: Why and How to Enrich the Logic of Research Questions. *Philos Theory Pract Biol* 14(0). <https://doi.org/10.3998/ptpbio.2100>
- Beatty J (1995) The Evolutionary Contingency Thesis. In: Wolters G, Lennox JG (eds) *Concepts, Theories, and Rationality in the Biological Sciences*. University of Pittsburgh Press, Pittsburgh, PA, pp 45–81
- Beatty J (1997) Why Do Biologists Argue like They Do? *Philos Sci* 64:S432–S443. <https://doi.org/10.1086/392620>
- Chase JM, Leibold MA (2003) *Ecological Niches: Linking Classical and Contemporary Approaches*. University of Chicago Press
- Chase JM, Myers JA (2011) Disentangling the importance of ecological niches from stochastic processes across scales. *Philos Trans R Soc B Biol Sci* 366(1576):2351–2363. <https://doi.org/10.1098/rstb.2011.0063>
- Chave J (2004) Neutral theory and community ecology: Neutral theory and community ecology. *Ecol Lett* 7(3):241–253. <https://doi.org/10.1111/j.1461-0248.2003.00566.x>
- Connell JH (1961a) Effects of Competition, Predation by *Thais lapillus*, and Other Factors on Natural Populations of the Barnacle *Balanus balanoides*. *Ecol Monogr* 31(1):61–104. <https://doi.org/10.2307/1950746>
- Connell JH (1961b) The Influence of Interspecific Competition and Other Factors on the Distribution of the Barnacle *Chthamalus stellatus*. *Ecology* 42(4):710–723. <https://doi.org/10.2307/1933500>
- Du X, Zhou S, Etienne RS (2011) Negative density dependence can offset the effect of species competitive asymmetry: A niche-based mechanism for neutral-like patterns. *J Theor Biol* 278(1):127–134. <https://doi.org/10.1016/j.jtbi.2011.03.003>
- Elliott-Graves A (2018) Generality and Causal Interdependence in Ecology. *Philos Sci* 85(5):1102–1114. <https://doi.org/10.1086/699698>
- Elliott-Graves A, Weisberg M (2014) Idealization: Idealization. *Philos Compass* 9(3):176–185. <https://doi.org/10.1111/phc3.12109>
- Elton C (1927) *Animal Ecology*. The Macmillan Company, New York
- Gause GF (1934) *The Struggle for Existence*. The Williams & Wilkins Company, Baltimore, MD
- Godfrey-Smith P (2009) Abstractions, Idealizations, and Evolutionary Biology. In: Barberousse A, Morange M, Pradeu T (eds) *Mapping the Future of Biology*. Springer Netherlands, Dordrecht, pp 47–56
- Gotelli NJ, McGill BJ (2006) Null Versus Neutral Models: What’s The Difference? *Ecography* 29(5):793–800. <https://doi.org/10.1111/j.2006.0906-7590.04714.x>

- Gravel D, Canham CD, Beaudet M, Messier C (2006) Reconciling niche and neutrality: the continuum hypothesis. *Ecol Lett* 9(4):399–409. <https://doi.org/10.1111/j.1461-0248.2006.00884.x>
- Griesemer JR (1992) Niche: Historical Perspectives. In: Keller EF, Lloyd EA (eds) *Keywords in Evolutionary Biology*. Harvard University Press, Cambridge, MA, pp 231–240
- Grinnell J (1917) The Niche-Relationships of the California Thrasher. *The Auk* 34(4):427–433. <https://doi.org/10.2307/4072271>
- Hubbell SP (2001) *The Unified Neutral Theory of Biodiversity and Biogeography*. Princeton University Press, Princeton
- Hubbell SP (2006) Neutral Theory and the Evolution of Ecological Equivalence. *Ecology* 87(6):1387–1398. [https://doi.org/10.1890/0012-9658\(2006\)87\[1387:NTATEO\]2.0.CO;2](https://doi.org/10.1890/0012-9658(2006)87[1387:NTATEO]2.0.CO;2)
- Hubbell SP (2005) Neutral theory in community ecology and the hypothesis of functional equivalence. *Funct Ecol* 19(1):166–172. <https://doi.org/10.1111/j.0269-8463.2005.00965.x>
- Hutchinson GE (1957) Concluding Remarks. *Cold Spring Harb Symp Quant Biol* 22:415–417
- Hutchinson GE (1961) The Paradox of the Plankton. *Am Nat* 95(882):137–145
- Jones MR (2005) Idealization and Abstraction: A Framework. In: Jones MR, Cartwright N (eds) *Idealization XII: Correcting the Model. Idealization and Abstraction in the Sciences*. Rodopi, Amsterdam, pp 173–217
- Justus J (2019) Ecological Theory and the Superfluous Niche. *Philos Top* 47(1):105–123. <https://doi.org/10.5840/philtopics20194716>
- Lange M (2013) Really Statistical Explanations and Genetic Drift. *Philos Sci* 80(2):169–188. <https://doi.org/10.1086/670323>
- Leibold MA, McPeck MA (2006) Coexistence of the Niche and Neutral Perspectives in Community Ecology. *Ecology* 87(6):1399–1410. [https://doi.org/10.1890/0012-9658\(2006\)87\[1399:COTNAN\]2.0.CO;2](https://doi.org/10.1890/0012-9658(2006)87[1399:COTNAN]2.0.CO;2)
- Leigh EG Jr (2007) Neutral theory: a historical perspective. *J Evol Biol* 20(6):2075–2091. <https://doi.org/10.1111/j.1420-9101.2007.01410.x>
- Levins R (1966) The Strategy of Model Building in Population Biology. *Am Sci* 54(4):421–431
- Levins R (1993) A Response to Orzack and Sober: Formal Analysis and the Fluidity of Science. *Q Rev Biol* 68(4):547–555. <https://doi.org/10.1086/418302>
- Levy A (2018) Idealization and abstraction: refining the distinction. *Synthese*. <https://doi.org/10.1007/s11229-018-1721-z>
- Longino HE (2006) Theoretical Pluralism and the Scientific Study of Behavior. In: Kellert SH, Longino HE, Waters CK (eds) *Scientific Pluralism*. University of Minnesota Press, Minneapolis, pp 102–131
- Longino HE (2013) *Studying Human Behavior*. The University of Chicago Press, Chicago
- MacArthur RH (1958) Population Ecology of Some Warblers of Northeastern Coniferous Forests. *Ecology* 39(4):599–619. <https://doi.org/10.2307/1931600>
- MacArthur RH, Wilson EO (1967) *The Theory of Island Biogeography*. Princeton University Press
- McGill BJ (2003) A test of the unified neutral theory of biodiversity. *Nature* 422(6934):881–885. <https://doi.org/10.1038/nature01583>
- Millstein RL, Skipper Jr RA, Dietrich MR (2009) (Mis)interpreting Mathematical Models: Drift as a Physical Process. *Philos Theory Biol* 1:1–13. <https://doi.org/10.3998/ptb.6959004.0001.002>
- Mitchell SD (2003) *Biological Complexity and Integrative Pluralism*. Cambridge University Press, Cambridge
- Mitchell SD (2002) Integrative Pluralism. *Biol Philos* 17:55–70

- Munoz F, Huneman P (2016) From the Neutral Theory to a Comprehensive and Multiscale Theory of Ecological Equivalence. *Q Rev Biol* 91(3):321–342. <https://doi.org/10.1086/688098>
- Odenbaugh J (2003) Complex Systems, Trade-Offs, and Theoretical Population Biology: Richard Levin’s “Strategy of Model Building in Population Biology” Revisited. *Philos Sci* 70(5):1496–1507. <https://doi.org/10.1086/377425>
- Odenbaugh J (forthcoming) Neutrality, Niche, and Nulls: Causal Relevance in Ecology. In: Waters CK, Woodward J (eds) *Philosophical Perspectives on Causal Reasoning in Biology*. University of Minnesota Press, Minneapolis
- Odenbaugh J (2005) Idealized, Inaccurate but Successful: A Pragmatic Approach to Evaluating Models in Theoretical Ecology. *Biol Philos* 20(2–3):231–255. <https://doi.org/10.1007/s10539-004-0478-6>
- Orzack SH, Sober E (1993) A Critical Assessment of Levins’s *The Strategy of Model Building in Population Biology* (1966). *Q Rev Biol* 68(4):533–546. <https://doi.org/10.1086/418301>
- Parker W (2014) Values and Uncertainties in Climate Prediction, Revisited. *Stud Hist Philos Sci Part A* 46:24–30. <https://doi.org/10.1016/j.shpsa.2013.11.003>
- Potochnik A (2017) *Idealization and the Aims of Science*. The University of Chicago Press, Chicago
- Rosindell J, Hubbell SP, He F, Harmon LJ, Etienne RS (2012) The case for ecological neutral theory. *Trends Ecol Evol* 27(4):203–208. <https://doi.org/10.1016/j.tree.2012.01.004>
- Strevens M (2004) The Causal and Unification Approaches to Explanation Unified-Causally. *Noûs* 38(1):154–176. <https://doi.org/10.1111/j.1468-0068.2004.00466.x>
- Tang J, Zhou S (2013) Hybrid niche-neutral models outperform an otherwise equivalent neutral model for fitting coral reef data. *J Theor Biol* 317:212–218. <https://doi.org/10.1016/j.jtbi.2012.10.019>
- Vellend M (2010) Conceptual Synthesis in Community Ecology. *Q Rev Biol* 85(2):183–206. <https://doi.org/10.1086/652373>
- Vellend M (2016) *The theory of ecological communities*. Princeton University Press, Princeton
- Weisberg M (2006) Forty Years of ‘The Strategy’: Levins on Model Building and Idealization. *Biol Philos* 21(5):623–645. <https://doi.org/10.1007/s10539-006-9051-9>
- Wennekes PL, Rosindell J, Etienne RS (2012) The Neutral—Niche Debate: A Philosophical Perspective. *Acta Biotheor* 60(3):257–271. <https://doi.org/10.1007/s10441-012-9144-6>
- Wimsatt WC (2007) *Re-engineering philosophy for limited beings: Piecewise approximations to reality*. Harvard University Press, Cambridge, MA
- Zhou J, Ning D (2017) Stochastic Community Assembly: Does It Matter in Microbial Ecology? *Microbiol Mol Biol Rev* 81(4):e00002-17. <https://doi.org/10.1128/MMBR.00002-17>