Published in: *Philosophy of Science* 66: 71-93 (1999)

THE AIM AND STRUCTURE OF ECOLOGICAL THEORY

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[‡] Most of this research was done at the Minnesota Center for Philosophy of Science and the University of Minnesota's Department of Ecology, Evolution and Behavior, both of which kindly provided a pleasant and stimulating environment. I wish to thank in particular John Beatty, Ronald Giere, Sara Tjossem and Kenneth Waters for exciting discussions and for critically reading earlier versions of this paper. I am also indebted to Eric Oberheim and the anonymous referees for helpful suggestions. This study was supported by the Swiss National Science Foundation.

Abstract

I present an attempt at an explication of the ecological theory of interspecific competition, including its explanatory role in community ecology and evolutionary biology. The account given is based on the idea that law-like statements play an important role in scientific theories of this kind. I suggest that the principle of competitive exclusion is such a law, and that it is evolutionarily invariant. The principle's empirical status is defended and implications for the ongoing debates on the existence of biological laws are discussed.

1. Introduction. Ecology today is frequently viewed as a science which, to the extent it succeeds, does not do so by discovering laws of nature, but by providing elaborate "case studies" (Shrader-Frechette and McCoy 1994; Sarkar 1996). In contrast, laws feature prominently in standard explications of the theory of evolution (e.g., Sober 1984). Why should evolution be lawful, and ecological processes not? Some philosophers, no doubt, would reject this question by arguing that laws in the traditional sense are not the right concept to describe scientific theories in the first place (Van Fraassen 1989; Giere 1995). Others deny specifically that there are laws of evolution, or of biology in general, given its subject matter (e.g., Beatty 1995). Only a few authors have attempted to rethink the concept of law in order to account for biological theories (Cooper 1996; Brandon 1998; Waters 1998). To date, little attention has been given to ecological theories in these debates.

My approach here is to examine what is probably the most highly developed theory of ecology, namely the theory of interspecific competition, with these questions in mind. I show that there are ecological laws, if it is allowed that laws generalize over a *restricted domain of application*, i.e., if they are construed as universally valid only within that domain, and inapplicable outside of it. I argue that this does not render these laws untestable or vacuous. From this I conclude that - contrary to current opinion in the philosophy of biology - a law-based construal of at least some ecological theories is viable, which might be of considerable interest for the recent debates on the metaphysical status of biological generalizations.

In section 2, I attempt to explicate the competitive exclusion principle in terms of a law-like statement with a restricted domain of application. I show that the principle, if understood properly, has empirical content. In sections 3 and 4, I examine the principle's explanatory role in community ecology and evolution. A discussion of the implications for John Beatty's Evolutionary Contingency Thesis concludes this essay.

2. The Laws of Competition. The theory of interspecific competition has considerably influenced ecological thought in the 20th century. After the pioneering mathematical work by A. Lotka and by V.Volterra and the laboratory experiments by G.F.

Gause and by T. Park (see Kingsland 1985 for an historical account and for references), competition theory was brought into center stage by G.E. Hutchinson's theoretical considerations on the conditions of coexistence of competing species in their ecological niches. As Hutchinson's presentation has been highly influential, I shall first give a brief account of it.

Hutchinson (1957) considered the range of environmental conditions in which a given species could persist indefinitely, i.e., under which the species has a reproductive rate that equals or exceeds its replacement level. He termed this range of conditions the *fundamental* or *preinteractive niche* of the species.[1] Since the different environmental variables that affect a species' rates of reproduction and mortality can be represented as dimensions in a Cartesian *n*-space, the fundamental niche can be thought of as a hypervolume in this space of environmental variables.

Next, Hutchinson considered what happens if two species S_1 and S_2 share a common habitat; the habitat he viewed simply as a volume B in ordinary physical space ("biotop space"). He noted that the Lotka-Volterra theory of interspecific competition entails that the two species can only coexist in a state of competitive equilibrium if the species' fundamental niches and their biotop space stand in a certain relation to each other. Lotka-Volterra theory starts from a logistic growth equation and introduces an additional density-dependent growth-limiting term for each competitor (see any ecology text for details). One of the crucial parameters in this theory is the coefficient of competition, which measures the growth inhibition the individuals of one species exert on those of another. It can be shown with elementary differential calculus that competing species can only coexist if each species has less inhibitory effect on the other than they have on themselves. Hutchinson reasoned that this will only be the case if the species' fundamental niches are somehow differentiated. Although Hutchinson did not treat the relationship between niche differentiation and competition coefficients quantitatively, such calculations were later carried out by others, e.g., by MacArthur and Levins (1967). Hutchinson now suggested that two species

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[1] Note that the fundamental niche à la Hutchinson is a dispositional property of a particular type of organism.

can only coexist in a state of competitive equilibrium if one of the following (mutually exclusive) conditions are met:

NDC1. N_2 is a proper subset of N_1 and S_2 is a superior competitor somewhere within the bounds of N_2 and parts of both niches are represented in B.

NDC2. $N_1 \cap N_2$ is a proper subset of both N_1 and N_2 (the fundamental niches overlap partially) and at least one non-intersection subset of the fundamental niches is represented in B. If one of the species has no non-intersection subset represented in B, it must be the superior competitor somewhere within the bounds of its niche (the latter case is similar to NDC1).

(N_i denotes the fundamental niche of the *i*-th species). I shall refer to these two conditions as Hutchinson's *niche differentiation conditions* (NDC). Hutchinson called the non-intersection subsets of NDC1 and NDC2 and the section of S_2's niche where it is a superior competitor of NDC1 *realized* or *postinteractive niches* of the two species in the presence of the other. NDC1 and NDC2 together imply that the species can only coexist if both species' realized niches are represented in the habitat, and that any two coexisting species' realized niches are non-intersecting.

Hutchinson's conjecture is a version of the *competitive exclusion principle* (also known as "Gause's principle", "Gause axiom" or "Volterra-Gause principle"). He referred to this principle as an "empirical generalization which may be verified or falsified" (1957, 418). Thus, Hutchinson thought that the competitive exclusion principle has *empirical content*.[2] Since this claim has been challenged, I shall first investigate whether it is justifiable.

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[2] Hutchinson appears to have changed his mind in his (1961, 138), calling the exclusion principle "analytically true." However, it doesn't seem that he was aware of the contradiction this forms with the claims he made in the 1957 paper. This suggests that he was not using "analytical" in the sense philosophers are accustomed to. He merely meant that the principle "can be deduced mathematically from a relatively simple series of postulates, which with the ordinary postulates of mathematics can be regarded as forming an axiom system" (1961, 137). In a later work, Hutchinson (1978, 238) writes about ecological theories: "As logico-mathematical statements, they are tautological; their biological interpretation, however, is not tautological and can be falsified." Since the same could be said of most physical

There are two main sources of potential trouble for the claim that the exclusion principle has empirical content. First, there is the suggestion that the failure of two species not satisfying NDC to competitively exclude each other can always be attributed to the ecologist's failure to detect a niche difference. Second, the principle can only be expected to hold under certain conditions, raising the problem of "ceteris paribus" conditions. I shall discuss these two problems in this order.

Slobodkin (1961) suggested that the competitive exclusion principle should not be viewed as an empirical generalization, but as a research heuristic:

> The Gause axiom is neither an empirical statement that is subject to empirical test [...] but rather a rule of ecological procedure [...]. Given a region of physical space in which two species do persist indefinitely at (or close to) a steady state, there exists one or more properties of the environment or species, or of both, that ensures an ecological distinction between the two species, and if one were to construct the multidimensional, fundamental niche of these two species a region would be found in this multidimensional space that is part of the fundamental niche of one of the two species but not of the other. If [the fundamental niches of the two species] seem identical the study is incomplete. Get more data! (123).

Slobodkin thus suggests that the failure of two coexisting competitors to show niche differentiation is no evidence against the competitive exclusion principle, it is merely evidence that the ecologist has not looked hard enough for them.[3] This attitude echoes a well-known study by MacArthur (1958), where a number of more or less happily coexisting warbler species with apparently identical habitat requirements turned out,

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theories, which are not usually considered to be "tautological", Hutchinson can't have meant that the competitive exclusion principle *itself* is an analytic truth, only that its *deduction* from some (empirical) premises is non-ampliative. Note that the Lotka-Volterra demonstration of the conditions for coexistence has to start from *empirical* assumptions about how populations expand and interact. If the premise of a deductive derivation is empirical, then so is the conclusion.

[3] Slobodkin did not mean to suggest that the principle is unimportant. However, others have used the alleged "tautological" character of the exclusion principle to question its theoretical importance (Peters 1976). The term "tautology", at any rate, is inappropriate, because the exclusion principle is clearly not a *logical* ('P or not-P'), nor a *conceptual* ('no bachelor is married') tautology. It isn't true by virtue of its logical form and the terms "competition", "coexistence" and "niche" are independently definable.

on close inspection, to show subtle differences in the way they forage in the canopy of trees. Evidently, if ecologists proceed strictly in the way suggested by Slobodkin, the competitive exclusion principle will never be refuted, and therefore has no empirical content, at least not in the Popperian sense of falsifiability.

However, except for orthodox Popperians, there is no need to identify empirical content with falsifiability. Many examples of theoretical statements are known to the philosopher of science which are never subjected to a Popperian test (Lakatos 1970). Theories sometimes contain a "protective belt" around a number of fundamental statements. In such cases, scientists will proceed exactly as Slobodkin wants ecologists to do: Recalcitrant observations will induce them to search for one or several false auxiliary assumptions in order to take the blame away from the fundamental theory (because it's indispensable for their research). And yet these fundamental statements can be seen as possessing empirical content in a wider sense than the Popperian one, namely in the sense that they can come into conflict with nature in some different way than the "naive falsificationist" prescribes. Hence, Slobodkin's suggestion that ecologists use the competitive exclusion principle as a research heuristic does not imply that it lacks empirical content.

Yet there is a sense in which the competitive exclusion principle, as formulated by Hutchinson, is a somewhat *weak* principle, and this might be the underlying reason for Slobodkin to see its sole use in guiding research.

The problem is that the principle in its Hutchinsonian formulation (NDC) says nothing about *how much* niche differentiation is required for the coexistence of competitors. Is, say, a 1% difference in the average size of seeds eaten by two bird species sufficient to allow for their equilibrium coexistence, or does it take at least a 50% difference? As long as information of this kind is not provided, the inferences licensed by the principle go only one way: From the fact of coexistence, infer the presence of a niche difference. In other words, NDC alone is only a *necessary* condition for coexistence. But since there might be cases in which the niche difference, although significant, is not enough to permit coexistence, NDC alone does not provide a sufficient explanation for coexistence.

For these reasons, ecologists have tried to come up with sufficient conditions for coexistence as well. What must be found is a niche difference which explains how the species meet the conditions for coexistence according to the Lotka-Volterra theory, or some other plausible theory of competition. In other words, a niche difference must be found that shows why the species will more inhibit their own growth than their competitors' (compare Hutchinson 1978, 198-203). This is usually not a trivial problem. Assumptions about the specific mechanisms of competition, about which Lotka-Volterra theory is silent, have to be introduced. An example is provided by Tilman's (1982) demonstration that two species of plants can only coexist on two limiting resources if each species consumes more of the resource that more limits its own growth (see section 3 for more details). Another way ecologists have approached this problem is by theories of the "limiting similarity" of coexisting competitors (see Abrams 1983 for a review). In this context, "similarity" is not morphological, but is defined in terms of the species' resource utilization and habitat requirements, although morphological differences ("character displacement") might be correlated with such niche differences. What these theories provide are conditions for the maximal "overlap" in the species' niches consistent with their equilibrium coexistence. They may be viewed as explanatorily crucial supplements to NDC. With their help, the principle can thus be formulated in the following way:

> *Competitive exclusion principle:* Species with insufficiently differentiated fundamental niches cannot coexist at equilibrium.

Whether this form of the principle has empirical content evidently depends on whether the vague term "insufficiently" can be filled out in a non-circular manner. Initially, ecologists were looking for *universal* limits to ecological similarity consistent with coexistence (May 1973, Chpt. 6). More recent work indicates that the limits to similarity are sensitive to various assumptions about the exact mechanisms of competition, i.e., they show *system specificity* (Abrams 1983). But this doesn't make the principle empirically vacuous. It only means that, in its most general form, the principle has a low information content (due to the vagueness of the term "insufficient" in the formulation above). However, in particular cases, the abstract principle can be instantiated to produce a statement with higher empirical content by providing more precise limiting similarity or "niche overlap" conditions.

The second major source of problems for the empirical nature of the competitive exclusion principle comes from that fact that the principle only holds under certain conditions. Hutchinson (1957, 417) briefly alluded to this problem by quoting Schrödinger's "restatement" of Newton's First Law of Motion: "a body perseveres at rest or in uniform motion in a right line, except when it doesn't." Hutchinson, like Schrödinger, may have been joking (although I'm not sure that he was). At any rate, the problem is that there are conditions allowing species to coexist even if they fail to meet niche differentiation and limiting similarity conditions. This problem is an instance of the well-known problem of so-called "ceteris paribus" laws which has considerably puzzled philosophers of science (e.g., Cartwright 1983; Hempel 1988; Giere 1995). I shall not discuss this vexing problem in its generality here; I only try to sketch a possible solution for the present context.

A crucial question is whether the conditions under which the exclusion principle will fail to hold can be *specified*. Hutchinson (1957, 417) suggested that this is the case by stating his belief that the principle "is true except in cases where there are good reasons not to expect it to be true." He discussed a number of cases where "the Volterra-Gause principle is unlikely to apply" (1957, 419f.).

One such case is if a species S_1 is a superior competitor to S_2 (i.e., S_1 will always displace S_2 if they encounter each other in a habitat), but S_1's dispersal rate is much lower than S_2's. If unoccupied patches open up randomly at a certain rate, the superior competitor S_1 will not be quick enough to seize them all. Those patches that escape colonization by S_1 provide colonization and survival opportunities for S_2, which disperses much faster. In this way, S_2 can become a "fugitive species" escaping competitive displacement by S_1, in spite of the latter being a superior competitor (Hutchinson 1957, 419). The net effect is that both species survive even if the similarity of their resource requirements would otherwise lead to the exclusion of S_2. Similar scenarios for the coexistence of competitors were later developed into theories of "patch dynamics" (e.g., Yodzis 1986).

Hutchinson considered another set of conditions under which the exclusion principle cannot be expected to hold: periodic environmental changes in the habitat, where the frequency of these changes has the same order of magnitude as the time it takes for competitive exclusion to run its course (1957, 420; see also section 3). If the competition process is periodically interrupted, e.g., by population reductions, competitive exclusion may not proceed to completion (compare Huston 1979).

Both of these, and many more similar scenarios that ecologists have thought of, share as a common feature that *environmental heterogeneity* prevents the community of competing species from attaining a state of competitive equilibrium. Another set of conditions that are able to overthrow the exclusion principle is provided by the common ecological phenomenon of *predation*. The basic mechanism is that a predator may keep the densities of mutually competing prey species at levels which are too low for competitive interactions to become effective (Lubchenco 1978).

These cases do not exhaust the list of conditions under which the competitive exclusion principle fails to hold. However, it should be clear from these examples that ecologists have been quite successful in spelling out conditions that restrict the principle's domain of application. It is important to note that these domain restrictions are not introduced *ad hoc* to hedge the exclusion principle in the face of recalcitrant evidence. Quite to the contrary, a considerable number of such conditions have been *predicted* on theoretical grounds.

In general, the procedure for such predictions is this. Recall that the competitive exclusion principle was originally derived from the Lotka-Volterra competition equations by introducing an *equilibrium assumption*, i.e., no change in population density for all competing species. This leads to the conditions for coexistence of the competing species, which are characterized by certain ratios of the coefficients of competition and the carrying capacities. Under any other conditions, on the equilibrium assumption, competitive exclusion will occur. Hence, the derivation of the competitive exclusion principle contains the equilibrium assumption as a premise. Evidently, if this assumption is relaxed, the competitive exclusion principle will not this assumption is relaxed, the competitive exclusion principle will not necessarily hold. In a second step, the theoretical ecologist has to show that certain conditions will prevent a system of competing species from reaching competitive equilibrium (thus justifying the relaxation of the equilibrium assumption). In the case of Hutchinson's solution to the paradox of the plankton, these conditions include seasonal variations in the species' physical environment. In the case of the ”fugitive species” scenario, these conditions involve dispersal of seeds and patch colonization. In the case of predation, as already mentioned, the predator keeps the densities of the competing prey species at levels at which competition is ineffective. Finally, it has to be shown that competing species with insufficiently differentiated niches will be able to coexist under the conditions investigated. This concludes the theoretical derivation of a domain restriction for the competitive exclusion principle. Thus, ecologists use models of interspecific competition (e.g., Lotka-Volterra) in conjunction with additional assumptions about an organism's ecological properties in order to *predict* conditions under which the competitive exclusion principle will fail.

At this point, an important objection has to be faced.[4] One of the main worries concerning laws is not whether *some* domain restrictions or “ceteris paribus-conditions” can be identified for biological (or, for that matter, physical) generalizations. What the criticism by Cartwright, Giere and others challenges is the possibility of *completing* this process. Therefore, citing a small number of known ceteris paribus-clauses - as I just did for the competitive exclusion principle - is no response to the criticism at issue.

While I am fully aware of the force of this objection, I think I have the resources here for answering it.

There appears to be a certain pattern in the various domain restrictions identified by ecologist for the competitive exclusion principle. All of them are describing mechanisms that prevent a system of interacting populations from reaching competitive equilibrium (see the previous paragraphs). While a complete *list* of such mechanisms may not be available at present, theory provides us with an *abstract scheme* for

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[4] This objection was raised by an anonymous referee.

all these mechanisms. Thus, ecologists possess a *theoretical understanding* of the kinds of conditions that render the competitive exclusion principle ineffective. Unless there are reasons to believe that the process of determining the generalization's domain of application will continue *ad infinitum* - which there are not in the present case - the domain of application seems reasonably well defined.[5]

As should have become obvious by now, I want to suggest that the competitive exclusion principle is a law-like generalization of competition theory. Under this view, there are a number of interesting properties which deserve attention.

First, the law's domain of application includes *organisms at all evolutionary stages*. It doesn't matter whether they reproduce sexually or clonally, whether they are small or large, "primitive" or "highly evolved." It applies even to quasi-species of replicating molecules (Maynard Smith and Szathmáry 1995, 34, 50). In other words, the principle is *evolutionarily invariant*. Second, using an important distinction introduced by Waters (1998), it is an example of a *causal regularity*, not a generalization about the contingent distribution of a biological property in the biosphere. In other words, it is not evolutionarily contingent in the sense of Beatty (1995). Furthermore, I suggest that it is an example of a *distinctly biological* generalization. The exclusion principle governs the coexistence of any systems that reproduce in a world of limited resources, and what could be more "biological" than that?[6] Readers familiar with the recent literature on biological laws will find this existence claim of distinctly biological but evolutionarily non-contingent generalizations particularly interesting. For this reason, it will be more fully discussed in the concluding section. Third, the law is *causally necessary*. It supports counterfactuals of the sort: 'If these two species

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[5] For deductivists, the main issue at stake behind the ceteris paribus problem is the deductive nature of theoretical inference (Hempel 1988). If any theoretical argument could succeed only via an infinite number of implicit ceteris paribus premises, this would be unsatisfactory in the extreme. However, a purely deductive account of theoretical inference is no longer generally accepted. For example, the deductive-nomological model of explanation is thought to be severely defective by most philosophers (including the present author) on grounds other than the ceteris paribus problem. In section 3, I shall use a contrastive account of explanation which involves laws, but which does not view explanations as simple deductions from such laws in conjunction with initial conditions. Hence, "fully dressed out ceteris paribus clauses to deduce the phenomena" (I owe this formulation to an anonymous referee) are not required.

[6] The distinctly biological character of ecological principles is not threatened by the fact that chemical entities like self-replicating molecules also fall under them, as self-replication is precisely where life begins.

were to compete for a single limiting resource, *ceteris paribus*, only one of them would survive.[7] The principle's nomic force, within its domain of application, is as strong as that of any deterministic law of physics.[8] No degrees of nomic force (cf. Cooper 1996, S33) need to be introduced.

It is not suggested here that the competitive exclusion principle is the *only* law-like generalization of competition theory. I have focused on the principle because of its central role in the development of ecological thought, and because of the interesting properties just mentioned. Furthermore, as I shall demonstrate in the following sections, the principle plays an important explanatory role in community ecology and evolutionary biology.

3. The Laws of Competition and Community Ecology. Community ecology seeks explanations for why particular groups of organisms are found living together in particular habitats. Ecologists may focus either on the overall species diversity, or on some subset of the inhabitants of an area, e.g., a guild (a group of species with similar resource requirements). The extent to which natural communities are, in fact, structured by competition is controversial (Diamond and Case 1986). This is an empirical question (with associated methodological problems) which I won’t go into. My aim in this section is, rather, to examine how purported explanations of community structure which are based on competition theory should be analyzed conceptually.

I shall begin by considering an uncontroversial example (if there is such a thing in ecology). In the 1930s, G. F. Gause performed a famous experiment on the unicellular organism *Paramecium* (see Kingsland 1985, 146-155). He grew different combinations of the three species *P. aurelia*, *P. caudatum,* and *P. bursarium* in microcosms containing bacteria and yeast cells as food sources, on which all three species reached high densities if grown in isolation. For two-species combinations, he found the following regularities: (1) *P. aurelia* always drove *P. caudatum* to extinction. (2) *P. cau-*

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[7] Interestingly, Mikkelson (1996) used the competitive exclusion principle to illustrate his theory of scientific counterfactuals.

[8] Of course, I do not mean to deny the existence or importance of *statistical* laws in ecology. However, the theories discussed here are fully deterministic.

datum and *P. bursaria* coexisted, but below their maximal carrying capacities. A closer examination of the second experiment revealed that the two populations were spatially separated: *P. caudatum* appeared to feed on the suspended bacteria, whereas *P. bursaria* grazed on the yeast cells at the bottom of the tubes.

Regularity (1) is readily explained by the competitive exclusion principle. Regularity (2) at first appears to be an anomaly, however, once the spatial separation is known, the coexistence can be attributed to niche differentiation. (2) is thus not an instance of the principle.

In this example, the competitive exclusion principle provides an explanation of why one two-species community is stable, whereas the other is not. The explanation given is simply a direct *application* of the principle itself.[9] The most straightforward analysis for such cases, I suggest, is to say that the principle functions as a law-like generalization which tells us that, under the given conditions, one of the two-species communities *had* to be unstable (by causal necessity).

The competitive exclusion principle's explanatory role in community ecology does not end here. I now would like to show that, strikingly, the principle can be part of an explanation even in cases where it *doesn't apply*.

Considering a community of species with highly similar resource requirements, an interesting question arises: Given that most resources are limited, how can a number of species competing for a set of limited resources coexist at all? As the famous "bottle" experiments by Gause, Park, and others have shown, artificial communities with several species competing for a single resource are inherently unstable. MacArthur (1972, 25) found these experiments "instructive because of their contrast with nature rather than their parallel to it." The explanation for the instability of these experimental systems, of course, is provided by Lotka-Volterra theory and the competitive ex-

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[9] From a contemporary point of view, of course, Gause's study is only fragmentary. A modern ecologist would want to demonstrate exactly that in case (1) the niche difference is too small for coexistence, whereas in case (2) it is sufficient (see Tilman 1977 for an example). However, the "bottle experiment" case contains all the elements of this basic type of competition-based ecological explanation that I wish to expose here. One of my referees found it remarkable that the most exemplary study of competition should be over 60 years old. I don't think this is uncommon for such textbook exemplars, and it should not be taken to mean that there has not been any progress in experimental studies of competition (see Connell 1983 and Schoener 1983 for two reviews of competition experiments).

clusion principle, but MacArthur's point stands: If the conditions for coexistence are so tight in laboratory experiments, how can diverse communities of competing species, as they are found in nature, be stable?

Hutchinson (1961) framed this question in terms of his "paradox of the plankton". Phytoplankton species basically require light, CO_2, and a number of inorganic salts for survival. Therefore, one would expect them to be in severe competition. Competition theory thus predicts that all but one species of algae in a freshwater lake community will go extinct. And yet there are usually many coexisting species of phytoplankton found in relatively small freshwater habitats. How could this be if the competitive exclusion principle is a true law-like generalization?

From what we have learned about the exclusion principle in the last section, there are different possible explanations: First, there might be hidden niche differences between the algae that allow their coexistence in a state of competitive equilibrium. Second, there could be a heterogeneous environment which prevents competitive exclusion. Third, coexistence could be promoted by predators. There might also be a combination of such mechanisms at work. The explanation suggested by Hutchinson was along the lines of environmental heterogeneity. He pointed out that freshwater lakes are subject to seasonal changes in various environmental variables. The critical question is now whether the time it takes for the community to reach a state of competitive equilibrium is in the same time scale as the time it takes for seasonal environmental change to take place. In this case, the process of competitive exclusion will be severely disturbed, and species with insufficient niche differentiation may coexist.

Hutchinson's solution to the "paradox of the plankton" is instructive for the structure of certain explanations in community ecology. In this kind of explanation, competition theory provides a background against which explanations are sought. To make this thesis more precise, I shall have to briefly discuss some general aspects of explanation.

Explanations can be viewed as answers to 'why?' questions (Van Fraassen 1980, 141-146). Such questions obtain their precise meaning from their context. Part of this context is provided by a *contrast class* containing the proposition that is to be explained. In general, a question 'why *P*?' is elliptical for 'why *P*, and not *P*, P**, ...*?'. The starred '*P*s' are propositions which are different from *P* and which, in contrast to *P*, are implied to be false by the question. They, together with *P,* form the question's contrast class. The answer to the question proceeds by citing a proposition (or conjunction of propositions) 'because *A*', where *A* bears an appropriate relevance relation *R* to <*P, P*, P**, ...*> and entails that *P* is the only true proposition in this *n*-tuple. If the question asks for a *causal* explanation (which presumably, is also determined by the context), *R* should be a relation of causal relevance.[10]

I suggest that in Hutchinson's explanation of plankton communities the competitive exclusion principle provides the contrast class for the explanation of the structure of the plankton community. The question the explanation answers is 'why are there many species of planktonic algae in freshwater lakes?'. This question is hard to answer; one doesn't really know where to start. But the question 'why are there many species of planktonic algae, rather than just one species: the superior competitor?' is much more precise. The contrast class is provided by the exclusion principle, which makes us expect all but one alga to go extinct. The explanation then proceeds by citing a causal mechanism - environmental variation - which shows how the algae can evade competitive exclusion.

The logic of this explanation of community structure is somewhat akin to certain explanations in classical mechanics. Newton's First Law of Motion states what happens to a body in the absence of forces. An explanation of the motion of a particular body, e.g., a planet, then proceeds by invoking a force which explains why the body in question is *not* at rest or in a state of uniform motion in a straight line. Similarly, in population genetics, the Hardy-Weinberg law describes a state of affairs which obtains in the absence of evolutionary forces (Sober 1984, 27-38), namely that gene frequencies will not change from one generation to the next. Explanations in population genetics then postulate forces to show how gene frequencies can change nevertheless. It may seem startling that these "zero force states" need not be realized anywhere in

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[10] To avoid trivialization of such an account of explanation, constraints need to be imposed on *R* (Kitcher and Salmon 1987). One possible way of doing this is to construe *R* as a causal relevance relation.

the universe, and yet the laws that describe them play an important explanatory role. Equally startling is the fact that there exist generalizations which are part of explanations of instances to which these generalizations do not *actually* apply. The reason, I suggest, is the contrastive nature of explanation.

So, my suggestion is that some explanations in community ecology invoke "forces" such as environmental heterogeneity or predation to show how groups of species with similar resource requirements evade competitive displacement by a superior competitor. This is reflected in the common community-ecological parlance of "mechanisms of coexistence", as well as in MacArthur's above-quoted comment about Gause's and Park's "bottle" experiments on competition being "instructive because of their contrast with nature." The competitive exclusion principle provides a counterfactual[11] community scenario for the case of absence of forces promoting coexistence, thus making coexistence *a phenomenon in need of explanation*.

A more recent example of this type of community-ecological explanation is provided by Tilman's (1982) theoretical work on resource competition in plant communities. Plants usually depend on a relatively small number of limiting resources including light, space, and nutrients such as inorganic phosphate and nitrogen. The diversity of plant species is therefore *prima facie* harder to explain than the diversity of animal communities, because the latter is in part explained by the diversity of the former. The competitive exclusion principle predicts that the maximum number of species that can coexist on a set of limiting resources is identical with the number of resources available. Yet the species richness of plant communities can be much higher than the number of limiting resources. As in the case of the plankton, the community ecologist looks for a mechanism that explains the stable coexistence of considerable numbers of plants in certain communities.

Tilman considered a hypothetical case in which there are two limiting resources which are consumed by a number of plant species. He showed that, in a homogeneous

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[11] Note that the exclusion principle's ability to support counterfactuals (section 2) is necessary for it to perform the explanatory role I am suggesting. Conversely, the principle's use in specifying a "zero force state" in ecological explanations may be viewed as evidence that it does, in fact, support counterfactuals.

environment, maximally two species can coexist at equilibrium (see Fig. 1). Coexistence is restricted to a region in the resource supply plane in which each species consumes proportionally more of the resource which more limits its own growth. This is exactly what one would expect from the competitive exclusion principle, for these conditions are analogous to the conditions for coexistence according to Lotka-Volterra theory, where coexistence is only possible if the individuals of each species compete more severely with their own kind than with individuals of the other species. However, Tilman's theory is more specific ("mechanistic," as Tilman is fond of saying) because it takes into account the mechanism of competition, namely depression of resource levels below the region that is critical for the maintenance of the other species.

If the condition of spatial homogeneity of the environment is relaxed, more than two species can coexist on the two limiting resources (Fig. 2). As in Hutchinson's "paradox of the plankton", the competitive exclusion principle suggests a "default" scenario which raises the question of why so many plant species can generally subsist on a small number of limiting resources. Theory then postulates a mechanism, in Tilman's case an interaction of resource competition and environmental heterogeneity, which explains how species can evade competitive displacement.

Other theories postulate periodic environmental disturbances (e.g., Huston 1979, Connell 1978) or predation (e.g., Lubchenco 1978) to explain the unexpected species richness of certain communities. This line of theoretical work in community ecology, which combines competition with other ecological processes such as environmental variability and predation, has somewhat departed from a tradition which sought to explain the structure of communities *entirely* in terms of competition and niche differentiation.[12] But the competitive exclusion principle still plays a role in these explanations as a background on which explanations are sought by way of "mechanisms of coexistence."

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[12] A famous example for the strategy to explain the structure of complex communities exclusively on the basis of competition and niche differentiation is Diamond’s (1975) controversial study of the New Guinea avifauna.

Of course, different explanations of community structure are not mutually exclusive. The applicability of an explanation to a particular instance depends on whether the conditions in that case are such that it falls into the theory's domain of application. Despite this, each theory "competing" for the status of an explanation of the structure of particular communities may feature distinct, suitably restricted law-like generalizations, such as "predation increases the number of coexisting competitors at the next lower trophic level", or "environmental heterogeneity allows more species to subsist on a set of limiting resources than there are resources" (note how these generalizations are only fully explanatory on the background of the competitive exclusion principle, as predicted by my account). A law-based account of ecological theories is therefore - appearances notwithstanding - fully compatible with a "pluralistic" approach to community ecology, as it is advocated in Diamond and Case (1986).

I am not suggesting that all explanations in community ecology have the structure outlined above. It applies only to cases in which ecologists consider groups of more or less stably coexisting organisms with similar ecological requirements, for it is in these cases in which competition is likely to play a role in shaping the community. But my account might to some extent explain why competition theory has drawn so much attention: Hutchinson's niche concept and the competitive exclusion principle has allowed ecologists to ask precise questions and come up with plausible answers.

4. The Laws of Competition and Evolution. In this section, it will be argued that the competitive exclusion principle also plays a significant role in evolutionary biology, namely theories of adaptive radiation. This explanatory role is somewhat different from its role in community ecology, discussed in the previous section.

The great ornithologist David Lack came to believe that the competitive exclusion principle plays a major role in evolution while reanalyzing his data on the Galápagos finches. These data were to become the empirical basis of his *Darwin's Finches* (1947), one of the most celebrated works in 20th-century evolutionary thought. When Lack first analyzed his finch data, he followed orthodox thinking at that time in that morphological differences between closely related species were believed to be nonadaptive (Ratcliffe and Boag 1982, xvii). On this view, the striking differences in beak morphology in sympatric finch species are coincidental, and the subtle differences in food utilization merely consequences of the differences in beak morphology. However, Lack wrote in *Darwin's Finches:*

> My views have now completely changed, through appreciating the force of Gause's contention that two species with similar ecology cannot live in the same region. This is a simple consequence of natural selection. If two species of birds occur together in the same habitat in the same region, eat the same types of food and have the same other ecological requirements, then they should compete with each other, and since the chance of being equally well adapted is negligible, one of them should eliminate the other completely. Nevertheless, three species of ground-finch live together in the same habitat on the same Galapagos islands, and this also applies to two species of insectivorous tree-finch. There must be some factor which prevents these species from effectively competing (Lack 1947, 62).

Lack thus recognized that the competitive exclusion principle suggests an evolutionary explanation for the evolutionary divergence of the finch species: competition for food between two recently split species (presumably they split in allopatry, but are now living in sympatry again) creates a selection pressure favoring those individuals that sufficiently differ from their competitors with respect to their food requirements. The latter are themselves a consequence of the beak size and shape, and therefore natural selection should act directly on these morphological features. Hence, selection drives sympatric species apart, rendering their interspecific differences adaptive. On this view, the shape of a beak in the finches is fine-tuned by natural selection to avoid competition with a species' closest relatives.

Lack reasoned that the physical conditions on the Galápagos islands were not sufficiently variable geographically to explain the character divergence in the finches (1947, 81, 117). Some additional evolutionary force driving species apart was required, and it was this that the competitive exclusion principle provided. Lack's account of speciation was therefore slightly different from Mayr’s (1942) classical theory, because, according to the latter, species acquire their major interspecific character differences in allopatry, whereas, according to Lack, a substantial part of these differences are acquired by competing species in sympatry (this should not be confused with a theory of sympatric speciation). It is today thought that Lack overlooked the possibility that the finches diverged in allopatry due to variability of *biotic* factors (i.e., the flora) on the Galápagos, but the outlines of his evolutionary explanation are still accepted today (Grant 1986, Schluter 1996).

We can now assess the role of the competition exclusion principle in theories of speciation. I suggest that the principle provides what Sober (1984, 50) has termed a *source law* for selection theory. Sober aptly distinguishes between consequence laws and source laws. The former describe how heritable fitness differences in a population cause changes in gene frequencies from one generation to the next, whereas the latter explain how such fitness differences are caused by differences in the organisms' physiology, behavior, and ecology. The competitive exclusion principle functions as a source law in theories of the adaptive radiation of closely related sympatric species. It explains why individuals which are sufficiently different from their competitors in terms of food requirements have a higher fitness value, namely because they are less likely to be competitively displaced. The source law takes the form of a law-like statement, such as 'ceteris paribus, individuals with different food requirements with respect to the individuals of a competing species have a higher fitness value.'

How different is the role of the exclusion principle in evolutionary biology from its role in community ecology? I have suggested (in section 3) that, in some cases, the principle's explanatory role is tied to the pragmatics of explanation. Here, the principle seems to play a more direct role, by being part of causal-explanatory statements proper. I have accepted the view that explanations are answers to questions of the form 'why *P*, rather than *P**, *P***, ...?', and that the answer has the form 'because *A*', where *A* is a conjunction of statements which are causally relevant to *P*'s being true and *P**, *P***, ... being false. In community ecology, it seems, the competitive exclusion principle provides one of the '*P**s', whereas in evolutionary biology, it provides a possible '*A*'. The contrast class in the latter case is provided by the theory of evolution. Evolutionary biology asks different questions than does community ecology: The latter asks how species communities are assembled from a pool of potential inhabitants available to a particular habitat, no matter how the habitat requirements of these colonizers evolved. In contrast, the former asks how species destined to live together in a habitat evolve over many generations under the influence of abiotic factors and biotic interactions such as interspecific competition. The explanatory contexts of community ecology and evolutionary biology should thus expected to be different.

5. Implications for the Debate over Biological Laws. In the preceding sections, I have tried to show that ecological theories, at least the theory of interspecific competition, can be construed as containing law-like statements as for example the competitive exclusion principle and other generalizations that feature in explanations of community structure and species formation. Furthermore, I have used a contrastive account of scientific explanation involving laws to explicate the explanatory role of the competitive exclusion principle in ecology and evolution. I have suggested that the exclusion principle is sometimes applied directly to explain the structure of communities or the ecological basis of adaptive evolution, and that in another class of instances, it provides something like a “zero force state”, i.e., a counterfactual scenario which picks out the relevant contrast class and the phenomena in need of explanation.[13] In this last section, I wish to discuss some possible consequences for the ongoing debate on the existence of biological laws.

Time and again, the philosophy of biology is stricken with outbreaks of lawlessness (Sober 1998), i.e., arguments to the effect that there are no biological laws. One of the most carefully argued examples is John Beatty's Evolutionary Contingency Thesis (Beatty 1995). Beatty argues that whatever generalizations appear in the con-

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[13] Waters (1990) has applied a similar idea to theories of ecological succession.

text of biology are either those of physics and chemistry, or they describe contingent outcomes of evolution in which case they lack the necessity or counterfactual-supporting force traditionally required of law-like generalizations. The main reason for this, according to Beatty, is the fact that the evolutionary process displays "high-level contingency", meaning that even under the same environmental conditions, selection pressures etc., evolution would take a species of organisms to a different adaptive peak (or to no adaptive peak at all, or the adaptive peaks might not even be the same) if it were rerun. This means that any biological generalization that holds in our world cannot be expected to hold in a possible world sufficiently different from ours in order to bestow law-likeness on it, and is therefore accidental. Frequently cited examples of contingent biological generalizations are the genetic code, which is widely seen as a "frozen" historical accident, or the most famous "laws" of biology: those associated with the name of Mendel, which are supposedly contingent on some rather strange historical accidents that led to the evolution of sex.

Kenneth Waters (1998) counters the Evolutionary Contingency Thesis by drawing a distinction between biological generalizations which describe the *distribution* of some trait among groups of organisms, and generalizations that describe *dispositions* or *causal regularities*. Using Waters's distinction, Mendel's laws (note the absence of scare quotes) could be interpreted as describing a disposition of organisms with a certain internal genetic/physiological makeup to pass on their genes in a certain way. Any organism with this internal genetic/physiological makeup has this disposition and will *necessarily* behave in this peculiar way, which renders Mendel's laws law-like. But Mendel's laws say nothing about the distribution of this disposition within the phylogenetic tree. This distribution is indeed historically contingent. In other words, the domain of application of Mendel's laws is a certain genetic/physiological type, and organisms from any region in the phylogenetic tree may contingently evolve into or out of this domain. Hence, the Evolutionary Contingency Thesis only applies to some biological generalizations, namely those that describe distributions, but not to others, namely those that posit dispositions and causal regularities.

To this move, Beatty (1995, 60-62) responds like this. He first accepts Waters's point that biological regularities such as Mendel's laws could, at least in principle, be rendered law-like (i.e., non-contingent) by specifying a natural kind in terms of the underlying physiological mechanisms, although he considers this to be difficult. But he then goes on to claim that such a reformulation will always destroy the laws' *distinctively biological* character, in other words, the laws transmogrify into physico-chemical ones. Thus, according to Beatty, there is some kind of a necessary trade-off between a regularity's law-likeness and its distinctively biological character:

> [T]he closer one's generalizations [...] come to describing sequences of chemical reactions, the more certain one can be that they are laws, because one can be more certain that no evolutionary outcomes can contradict them. But at the same time, the generalizations will become less and less distinctively biological (Beatty 1995, 62).

Indeed, Waters's (1998, 19) example of a law-like causal regularity, "Blood vessels with a high content of elastin expand as internal fluid pressure increases [...]", is vulnerable to exactly this Beattian objection. Waters views this as a *biological* law-like statement, where "blood vessels" refers to a somewhat sloppy natural kind defined by the shared internal make-up of these anatomical structures. But Beatty will view it as a disguised *physical* law about a certain kind of macromolecular aggregate, where the disguise is provided by the biological term "blood vessel". According to Beatty, as soon as one tries to specify the "shared internal makeup" of these structures in order to pick out their causal dispositions, one will end up with molecules, and thus leave the distinctively biological realm.

What are the implications of my conclusions with respect to ecological generalizations for this debate? What I would like to suggest is that cases like the competitive exclusion principle are clear-cut counterexamples to Beatty's strategy to drive a wedge between the law-likeness and the distinctively biological character of a generalization. They provide positive instances for Waters's account of causal regularities. For, as I have argued, ecology knows evolutionarily invariant generalizations which are law-like, and at the same time distinctively biological.

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FIGURES

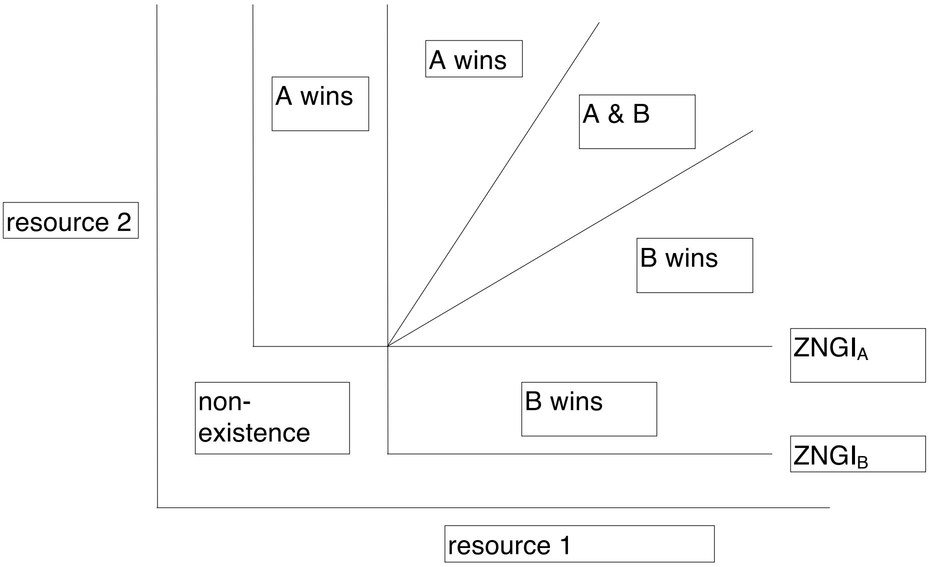

Fig.1. Two species, two resources. The two axes represent the supply rates of two limiting resources. The zero net growth isoclines (ZNGI) of two species A and B indicate the supply rates at which the species will maintain a stable population density. In the area labelled 'A wins' to the very left, B cannot exist. In the area right next to it, both A and B can exist in the absence of the other, but if A is present, it will reduce the supply of resource 1 to a level at which B cannot exist and therefore "wins" the competition (competitive displacement). In the area labelled 'A & B' both species can coexist in an equilibrium state. The other areas are analogous. Three species cannot coexist in this hypothetical situation. (After Tilman 1982.)

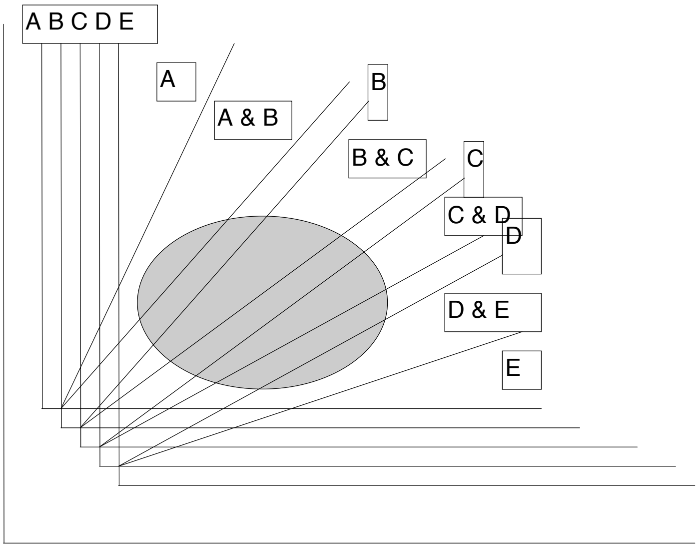

Fig. 2. Coexistence of five species on two limiting resources. No single supply point can support more than two species at the same time, but a heterogeneous environment containing microenvironments providing a range of supply rates (represented by the blotch) of the two resources can support five or more species. (After Tilman 1982.)