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Ecological Laws and Their Promise of Explanations
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Marcel Weber (1999) argued that the principle of competitive exclusion is a law of ecology that could explain phenomena (1) by direct application, or (2) by describing default states. Since he did not offer an account of explanation by direct application of laws, I offer an interpretation of explanation by direct application of laws based on a proposal by Elgin and Sober (2002). I show that in both cases it is the descriptions of mechanisms that explain phenomena, and not the laws. Lev Ginzburg and Mark Colyvan (2004) argued Malthus' Law of Exponential Growth is the first law of ecology, and that its role explanations is to describe default states. I argue the role of the descriptor of default states is not necessary for ecological explanations, and the descriptions of underlying mechanisms offer the required explanations. Additionally, I examine the possibility not considered by Ginzburg and Colyvan that Malthus' law could explain the phenomena of exponential growth by direct application. I also show that this explanation is inferior to the descriptions of underlying mechanisms.

Keywords: ecology, explanation, laws, mechanisms, models.

Ecological Laws and Their Promise of Explanations

1. Introduction

In contrast to the student of physics, the student of ecology is not taught her/his science offers an unequivocal set of laws that should be used to explain and predict ecological phenomena. Moreover, important voices in the philosophy of biology argue that explanation in biology is not about applying laws, but about discovering mechanisms (Darden 2006; Bechtel 2006) and causal relations (Darden 2006, Bechtel 2006, Woodward 2003, Woodward 2010). Yet several ecologists and philosophers of science have argued that ecology has laws (Colyvan and Ginzburg 2003b, Ginzburg and Colyvan 2004, Weber 1999, Turchin 2001, Berryman 2003, Mikkelsen 2003, Lange 2005, West and Brown 2004, Cooper 2003), and some have even argued that it is analogous to physics (Colyvan and Ginzburg 2010).

Proponents of the laws of ecology offer converging arguments that converge on denying an understanding of the laws of ecology modeled after the laws of physics. Gregory Cooper (2003) shows the traditional concept of law prevents us from acknowledging the laws of ecology, and we need to replace it with one that accounts for the explanatory and predictive practice of ecology. Such a concept should acknowledge that lawfulness is a matter of degree and of invariance over a range of possibilities (Cooper 2003, 113-114). Mark Lange (2005) argues that ecological laws are invariant over a range of changes in the microphysical states that realize them. This makes ecological laws autonomous from microphysical states and prevents ecological explanations from being reduced to explanations of physics. To recognize the laws of ecology, we need to clear up some misconceptions about the laws of physics: they are not

exceptionless, do not make precise predictions, and cannot be mere regularities, say Mark Colyvan and Lev Ginzburg (2003b). Marcel Weber argues if it is acknowledged 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” (Weber 1999, 72) and given that the competitive exclusion principle holds universally within its domain, it follows that it is a law of competition theory.

Ginzburg and Colyvan were the first to support the view that Malthus’s law is a law of ecology; Peter Turchin (2001) and Alan Berryman (2003) followed in accepting this perspective. The law states that “the rate of change of population abundance, with respect to time, is proportional to population abundance” (Colyvan 2008, 304), or $dN/dt = rN$. The law is also expressed by the exponential growth equation that is usually known as the Malthus Law: $N(t) = N_0e^{rt}$ (Colyvan 2008). Weber (1999) argues the principle of competitive exclusion would be another law of ecology. The principle states: “species with insufficiently differentiated fundamental niches cannot coexist at equilibrium” (Weber 1999, 76).

In this essay, I examine the laws of Malthus, and of competitive exclusion, and their roles in ecological explanations. I focus on these two laws because their proponents formulate accounts of the roles of the laws in explanations. Moreover, these proposals of laws can be seen as representative examples since their law-like character is generally acknowledged. The list of propositions presented as laws is longer, though,¹ which

¹ Ginzburg and Colyvan (2004) think that ecological allometries, which are “statistical regularities that hold between various biological and ecological quantities” (12), are good candidates for laws of ecology. Kleiber allometry is an early, representative example of allometries. It shows that basal metabolic rate is proportional to a $3/4$ power of body weight. Other allometries are those discovered by Fenchel, Damuth, and Calder

further shows that the case for laws in ecology merits attention. My findings could apply to these other proposals of ecological laws. I examine a possible way in which laws could be seen as providing explanations, and show ecological laws have a derivative explanatory capacity, at best, and descriptions of mechanisms offer the desired explanations.

2. Ecological Laws Explain by Direct Application

While the goal of ecologists is to show that ecology has genuine laws is tied to their concern to demonstrate it is a science on a par with physics, philosophers of science examine this issue with an emphasis on the role of laws in ecological explanations. Following a distinction by Weber (1999, 81), the laws of ecology play two explanatory roles. First, they are part of covering-law style explanations. Second, they describe a default state and that description is used to formulate explanations that appeal to causal processes.

(Ginzburgh and Colyvan 2004, 16-21). Allometries are analogous to Kepler's laws. They are predictive, but not explanatory. Investigation into the basis of allometries takes the researcher to lower levels of biological and physical world (Brown et al. 2004, West, Brown, and Enquist 1997). Lange (Lange 2000, 2005) identifies three examples of ecological laws: Liebig's law of the minimum, the law of constant final yield, and the 3/2 thinning law, and the area law from island biogeography. Greg Mikkelson (Mikkelson 2003) argues that ecology is primarily a law-oriented science and thinks that two law-like generalizations that refer to structural kinds are laws of ecology. In addition to Malthus's law, Berryman (Berryman 1999, 2003) shows that ecology uses laws that cover intra-specific cooperation, competition, predator-prey interaction, and limiting factors acting on a population, such as Liebig's law of the minimum. He is one of the few that claims that these laws are not specific to ecology, but are reformulations of principles from general systems theory. Ecology is an integrative science that borrows from complex integrative systems, physics and chemistry (Berryman 2003, 700). Turchin (2001) adds the law of self-limiting growth of populations and consumer-resource oscillations (20-22).

2.1. An Interpretation of Explanation by Direct Application of Laws and Resulting Issues

Weber was probably the first to argue that ecological laws function in covering-law explanations. Similar arguments were offered by Lange (2000) and Mikkelsen (2003); therefore, my findings also might apply to their proposals. Weber contends the principle of competitive exclusion explains by direct application to a situation where competitive exclusion obtains regularly, i.e., when a species always drives another species to extinction. He illustrates such a case with the experimental work of G. F. Gause on paramecia, which showed that (1) *P. aurelia* always drove *P. caudatum* to extinction, while (2) *P. caudatum* and *P. bursaria* coexisted. The law easily explains regularity (1) that is an instance of the principle, but not regularity (2) which is not an instance. Weber's description of the explanatory role of the principle applied to the first regularity is limited to the following: "The explanation given is simply a direct *application* of the principle itself. 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)" (Weber 1999, 81). I interpret this brief description as a proposal to understand the role of the principle of competitive exclusion in terms of the deductive-nomological account.

Stated in the deductive-nomological form, this principle yields the following schema:

Explanans:

Law1: The principle of competitive exclusion: species with insufficiently differentiated fundamental niches cannot coexist at equilibrium.

Antecedent condition, i.e., description of "the given conditions":

C1: insufficiently differentiated niches of *P. aurelia* and *P. caudatum*, which could be further specified as the fact that they consume the same source of food, yeast cells, in a homogeneous environment;

C2: differentiated niches of *P. caudatum* and *P. bursaria*, which feed on different organisms and in different parts of the environment.

Explanandum:

P. aurelia always drives *P. caudatum* to extinction, but *P. caudatum* and *P. bursaria* coexist.

If the explanandum were the fact that *P. aurelia* always drives *P. caudatum* to extinction, its explanans would consist of the same law of competitive exclusion and antecedent condition C1, yet without antecedent condition C2.

A conception of ecological explanation formulated along the lines of Hempel's (1965) DN model, as implied by Weber's perspective on the application of laws for explanatory purposes, poses some issues. First, Weber's proposal does not do justice to how ecologists use models to describe and explain specific facets of the world; this includes Gause's account of competitive exclusion which he cites as a representative example to formulate his perspective on the role of laws. In various sciences, including ecology, scientists use models to formulate predictions that they hope will agree with the data obtained from interaction with the world. Should the prediction agree with the data, one concludes that the model most likely fits the world. The model would be rejected if its prediction does not agree with the data. Typically, the prediction does not match the data exactly, but it closely approximates the expected data. Of the many models that yield predictions, scientists would choose those models whose predictions better match the data, and the model would be best fitting.² Secondly, Gause's research implemented this epistemological conception long before philosophers articulated it. In his words, "The quantitative expression of the growth of population must go hand in hand with a direct study of the factors which control growth. Only in those cases, where the results deduced from equations *are confirmed by the data obtained through entirely different methods, by*

² For a more detailed account see Giere (1999, Giere, Bickle, and Mauldin 2006).

a direct study of the factors limiting growth, can we be sure of the correctness of the quantitative theories” (Gause 1934, 58). After having performed a number of experiments, Gause concludes: “the process of competition under our conditions has always resulted in one species being entirely displaced by another, in complete agreement with the predictions of the mathematical theory” (1934, 103). The mathematical theory he refers to are the Lotka-Volterra equations of competition, which is the model used to derive the prediction that there is no equilibrium between competing species occupying the same “niche” and that one of them will be displaced (Gause 1934, 48). Considering this, it is more appropriate to understand the explanation of competitive exclusion not in terms of the application of a law, but in terms of the fit between the model and experimentally obtained data. This conclusion extends to other investigations of competitive exclusion in laboratory conditions. For example, Vandermeer’s (1969) work on competition offers another good illustration of this approach centered on models. He used models to predict the growth of populations of four protozoans in monoculture, in two-way competition and in four-way competition. He then compared data obtained from laboratory experiments with what was expected based on models. In most cases, there was good fit between prediction and data.

The second difficulty that the DN account applied to competitive exclusion faces is that some ecological explananda present themselves as precise numeric values that do not follow deductively from the explanans. For example, the actual size of population A is 325 individuals, and population B is 3; however, the number that follows from the explanans is 333 individuals of A and 0 of B. The difference could be attributed to various accidental factors, but that would make the explanation probabilistic.

Alternatively, the explanation could be reconstructed according to the inductive-statistical model, which would require a probabilistic law, but the principle of competitive exclusion is causally necessary and within its restricted domain, the law has deterministic force (Weber 1999, 80). These types of results are found in the work of Vandermeer, who continued Gause's laboratory experiments and used his equations of competition to make precise predictions about the trajectory of population growth. The prediction for *P. bursaria* is that it will be eliminated, yet the observed data showed that it continues, although at a lower density. Vandermeer did not reject the model used to make the prediction because the general trend of the data agreed with predictions from the model. He cited "unknown but insignificant frictional components or excessive inherent variability" responsible for the mismatch between observed data and prediction (Vandermeer 1969, 367). Since the outcome of these examples—the general trend—very closely approaches competitive exclusion, one would expect the principle of competitive exclusion to explain it by direct application as illustrated above. However, explanation by direct application presents the second difficulty.

2.2 An Alternative Proposal of Explanation by Direct Application of Ecological Laws

To address the aforementioned difficulties and to account for the explanatory role of laws of ecology, I adopt a proposal by Elgin and Sober (2002) on explanation that Bokulich (2011) calls *covering-law model explanation*. Elgin and Sober argue that the explanans explains the explanandum "not by entailing it or by conferring a probability on it (high or low), but by showing that the value described in the explanandum is close to the value predicted by the idealization" (Elgin and Sober 2002, 448). The explanans must

contain (a) descriptions of the initial conditions, and (b) an idealized model.³ They use optimality models to illustrate their proposal:

- (i) Idealized law entailed by the optimality model: “If organisms are fitter the closer they are to the optimal value α and if no forces other than selection are at work in the population, then the population will evolve to a state in which all organisms exhibit the trait value α .”
- (ii) Partial description of initial conditions: “Organisms are fitter the closer they are to the optimal value α .”
- (iii) Observed facts: “The n organisms in the population have trait values $\beta_1, \beta_2, \dots, \beta_n$ (where each β_i differs only negligibly from α).” (Elgin and Sober 2002, 447)

Propositions (i) and (ii) explain (iii) in the sense that they show that the value described in (iii) is close to that predicted by (i) and (ii). Propositions (i) and (ii) do not make up a complete explanation, since they do not describe all causally relevant factors; nonetheless, they are explanatory (Elgin and Sober 2002, 447). There is more to this explanatory relationship when it is examined from the viewpoint of the model explanations account attributed to Bokulich (2011). The model plays a central role in this account, and its explanatory role is grounded in its ability to represent the pattern of counterfactual dependence specific to the target system. Given this counterfactual isomorphism, the model—together with the description of the antecedent conditions, and the resulting prediction—can provide information about how the investigated system would behave if the elements of the model were changed in various ways (Bokulich 2011, 39). Bokulich cites only the model as a provider of explanatory information, but I include

³ Elgin and Sober require that the idealized model entail a conditional that is an idealized law whose antecedent does not apply to any real world system. This requirement follows from their use of optimality models that assume infinitely large populations. Since ecological models assume finite populations, I would relax this requirement. Ecological models entail antecedents that apply to real world system.

the description of antecedent conditions and the prediction because the model must be interpreted to link it to the examined system, and both interpret the model.

When applied to the case of competitive exclusion described by Gause and examined by Weber, the covering-law model account yields the following reconstruction of ecological explanations that use laws, or law-like generalizations and models that express them:

- (i) Law1 entailed by the Lotka-Volterra equations of competition: If the species have insufficiently differentiated fundamental species, then they cannot coexist at equilibrium.
- (ii) C1: *P. aurelia* and *P. caudatum* occupy the same niche; they consume the same source of food, yeast cells, in a homogeneous environment;
C2: differentiated niches of *P. caudatum* and *P. bursaria*, which feed on different organisms and in different parts of the environment.
- (iii) Prediction based on (i) and (ii): *P. aurelia* will eliminate *P. caudatum*, while *P. caudatum* and *P. bursaria* will coexist.
- (iv) Data obtained from experiments: *P. aurelia* always drives *P. caudatum* to extinction, but *P. caudatum* and *P. bursaria* coexist.

Propositions (i) through (iii) provide information about how the target system would behave given changes in the model and in the initial conditions. In light of this, (i) and (ii) explain (iv) by showing that (iv) agrees with prediction (iii) derived from (i) and (ii).

Elgin and Sober's proposal might work for evolutionary theory, but one might still object that its application to competitive exclusion does not convincingly produce a covering law explanation. The problem is with proposition (i). Recall that Bokulich claims models involved in covering-law model explanations express laws, and they also represent counterfactual dependencies specific to the target system. I continue this line of reasoning and maintain that the reason counterfactual dependencies are able to characterize the target system is because it is a mechanism. Stuart Glennan (2002) offers this definition of mechanisms that supports my claim:

(M) A mechanism for a behavior is a complex system that produces that behavior by the interaction of a number of parts, where the interactions between parts can be characterized by direct, invariant, change-relating generalizations. (Glennan 2002, S344)

The direct, invariant, change-relating generalizations characterize counterfactual dependencies between the parts of the mechanism and the model of the mechanism, or the system represents these dependencies. Regarding the laws, I do not characterize them as exceptionless regularities of unrestricted scope, but only regularities of restricted scope. This characterization of laws is more appropriate for the principle of competitive exclusion since it has exceptions, as Keddy (2001) has shown. Regularities themselves are regular behaviors produced by mechanisms. Stated differently, the consistent operation of a mechanism produces a regularity that is described as a law. By virtue of representing the counterfactual dependencies between the parts of the mechanism and its behavior, a model also expresses a law. This entails that the law of competitive exclusion stated in proposition (i) has a derivative explanatory role derived from the mechanism that produces competitive exclusion. To explain why *P. aurelia* always drives *P. caudatum* to extinction, but *P. caudatum* and *P. bursaria* coexist, we need to describe the underlying mechanism. The principle of competitive exclusion simply states that a regularity occurs, but it does not tell us why it happens. In Glennan's terms, the principle of competitive exclusion is a mechanically explicable law. Shifting the explanatory role from the laws of restricted scope to the underlying mechanisms is also consistent with Gause's approach, and with later ecologists. Gause sought to identify the specific conditions that prevent the coexistence of *P. aurelia* and *P. caudatum*, but favor co-occurrence of *P. caudatum* and *P. bursaria*. These conditions of differential feeding behavior are key components of the mechanism of competitive exclusion. Since the

conditions occur regularly, competitive exclusion happens on a regular basis as well, and the principle states that.

2.3 Malthus' Law in Covering-Law Model Explanations

According to Ginzburg and Colyvan, Malthus' Law describes a default state from which actual ecological conditions depart, and ecological mechanisms explain this departure. I examine this role in Section 3.1. Supporters of the laws of ecology could argue that the Law of Exponential Growth explains by direct application to those cases that exhibit exponential growth, even if Ginzburg and Colyvan do not ascribe this explanatory role to Malthus' Law. In Section 2.3, I examine this possibility.

Presumably because “populations do not grow exponentially for long (if at all)” (Colyvan 2011, 304), Colyvan and Ginzburg do not explore those cases where Malthus' Law does not just describe a default state that does not occur, but plays a more comprehensive role in explanations of exponential growth in natural populations. Such growth happens in invasive species (Rockwood 2006) or in those cases where predation and interspecific competition are absent (Gotelli 2008). To help illustrate the argument, I use an example of exponential growth in the wild based on Gotelli (2008), but with slight modifications.

In 1937, time t_0 , eight pheasants were introduced onto Protection island, close to the coast of the Washington State, that had abundant food resources and lacked predators. Distance between the island and the coast precluded migration. By 1938, t_2 , the population increased to 30 birds, and to 1989 by 1942, although the exponential growth model predicted 5933 birds. The population grew exponentially the first three years. Ecologists' explanation of the growth of this population fits the covering model account.

From the model of exponential growth, $N(t) = N_0 e^{rt}$, and given the estimated finite rate of increase $\lambda = N_{t+1}/N_t = (30/8)=3.75$, and the rate of increase r as $\ln(3.75)=1.3217$, one deduces a prediction of the population size at the time of interest, say, 1940, to be 421. The actual population size is 418.

The model and the initial conditions explain the observed data by showing that the derived prediction matches actual data, and how the observed data could have changed if the rate of increase or the initial population size been different. Ecologists do not try to deduce the actual size of the population from Malthus' Law and a description of the antecedent condition, which make up the explanans. Strictly speaking, the value 418 does not follow deductively from the explanans. For this value to follow deductively, one would have to revise the explanans and add an extra premise specifying the deterministic cause of the death of the three birds. This move would be inconsistent with the actual practice of ecologists, who are content with getting a close fit of the model prediction with the data. Moreover, the causes of the death of three birds that account for the mismatch between prediction and the actual data would be probabilistic, similar to the previously examined case of competition, which would require reconstructing the explanation according to the inductive-statistical model. This approach requires a probabilistic law, however, this is not the case with Malthus' Law.

Population growth after 1940 significantly diverges from the model predictions. To explain the population size after 1940, the exponential model needs to incorporate the depletion of the food resource, which would make it logistic. As before, this would assume the initial conditions of no predation, no inter-specific competition, and no environmental disturbances. The logistic model would be explanatory as described above.

In reality, by 1943, there were no pheasants on the island. Their population size abruptly decreased to zero because the U.S. Army set up camp on the island and the soldiers ate the birds.

One could formulate to this interpretation of the explanatory role of Malthus' law the same objection that was raised to the explanatory role of the principle of competitive exclusion. The Law of Exponential Growth and the associated model only describe a tendency of a population to grow under certain conditions. The explanatory force of the law and of its model derives from the mechanism that produces the regular behavior of exponential growth. The mechanism consists of groups of birds of different genders that reproduce and die at certain rates and certain ages, the abundance of resources, the lack of migration, and the absence of competitors and predators—wolves, foxes, or homesick soldiers. It is the regular interaction between birds of different genders, the absence of migration, of interaction with competitors and predators that produces the exponential growth. An ecological explanation would specify all them. However, the model is incomplete. It contains only population abundance, time, and population growth rate, but not the other ecologically relevant factors. That the mechanism has explanatory priority is shown by the fact that one can explain exponential growth by referencing its parts and how they interact without using the model. But one cannot explain the exponential growth with the mathematical model and without linking it to the mechanism. The mechanism is sufficient to explain exponential growth, but the model is not. The model affords good predictions, but provides incomplete explanations.

3. Ecological Laws as Descriptors of Default States

Discussions of laws of ecology rely on an analogy with Newton's first law: In the absence of forces acting on an object, the acceleration of the object is zero (Serway and Jewett 2008). The analogy serves two purposes: 1) to argue that ecology has laws (Colyvan and Ginzburg 2003), and 2) to describe the role of these laws in explanations (Weber 1999, Colyvan and Ginzburg 2004). Following this analogy, Colyvan and Ginzburg, and Weber identify different laws of ecology, yet they see them as playing the same role as descriptors of a default state. This is the second role that laws of ecology play in explanations.

3.1 Ginzburg and Colyvan on Laws as Descriptors of Default States

Ginzburg was the first to argue that Malthus' Law is analogous to Newton's first law. The Malthusian Law is the only formula in population dynamics for which he accepts applying the term "law"; all the other formulas are models (Ginzburg 1986). Ginzburg developed this argument in a series of articles and in a book co-authored with Colyvan (Colyvan and Ginzburg 2003b, a, Colyvan and Ginzburg 2010, Ginzburg and Colyvan 2004). They propose a research program for ecology modeled after Newtonian principles. Just like Newton's first law, Malthus' Law describes a default state of a growing population when no disturbing forces are present. Analogously to the second law of classical physics that defines the concept of force as a quantity resulting in acceleration, Ginzburg and Colyvan "*define* 'ecological forces' as quantities that act on growing (or declining) populations as second-order quantities – 'ecological accelerations'" (Ginzburg and Colyvan 2004, 101). Considered together, the two laws of physics initiate a research program aimed at identifying the forces that exist in nature. Analogously, Malthus' Law

and the definition of ecological forces open up a research program to identify ecological forces that affect the dynamics of populations. Ginzburg and Colyvan examine three such ecological forces: energetics (the balance of metabolism and consumption), the maternal effect (the effect of the endowment of mothers on their daughters), and predator-prey interactions, the research program being open to other ecological forces.

Before further examining Ginzburg's and Colyvan's proposal, we need to clarify certain terms. They use the term "ecological force" as part of the analogy to physics. Throughout their work, they also use the terms "cause" and "mechanism" instead of "ecological force" to refer to entities that change population dynamics. I will use only the term "mechanism."

Populations rarely grow exponentially. More often their growth is influenced by various ecological forces, and the resulting population dynamics is described better using other models, such as the logistic model or the predator-prey model, which are central components explaining these population dynamics. Maternal effect is a key mechanism influencing the growth of a population; it causes inertia in population dynamics, as follows: "A population growing on a constant flow of resources and growing to its equilibrium value will not stop at that value but will overshoot the equilibrium. The reason is that mothers reproducing when the population is below equilibrium abundance have plentiful resources and their daughters' reproduction responds not only to daughters' current conditions but also to the conditions their mothers experienced. The same happens when populations decline from a higher abundance to the equilibrium: in this case, mothers were overabundant and thus undernourished. The resulting effect on daughters leads to the undershooting of the equilibrium abundance. Maternal effect can

thus easily lead to populations oscillating about the equilibrium value” (Ginzburg and Colyvan 2004, 50). When this maternal effect is incorporated into the exponential growth equation, it yields a model comprised of a pair of equations; the first one is a logistic growth equation:

$$\begin{aligned} N_{t+1} &= RN_t f(X_t) \\ X_{t+1} &= X_t g\left(\frac{S}{N_{t+1}}\right) \end{aligned} \quad (1)$$

The maternal effect model assumes non-overlapping generations. N is population abundance, X is the average individual quality, while parameter R is the maximum population growth rate of individuals of very high average quality. R is assumed to be greater than 1. If $R < 1$, the population will decline; t represents time in generations; f is a monotonically increasing function of quality, X , while g is a monotonically increasing function of per capita food, S/N_{t+1} (Ginzburg and Colyvan 2004, 50-51).

Ginzburg and Colyvan do not offer an account of how the model works, but we can understand its explanatory role based on its usage. Ginzburg and Taneyhill (1994) used the model to predict the dynamics of six populations of different forest moth species. They compared predictions with observed data on population cycles of those species, and they found out that predictions of the model fit very well with the observed data. Given this fit between predictions and observations, Ginzburg and Taneyhill concluded the model of the maternal effect mechanism might explain the population cycles. This finding indicates that Malthus’ law does not explain the observed dynamics of populations. Moreover, its role in ecological explanations is questionable.

According to an influential view among ecologists, the goal of ecology is to study “the interactions that determine the distribution and abundance of organisms,” (Krebs 2008, 5), and which are observed. The six populations of moth species serve as an

example of the distribution and abundance that ecology studies. The maternal effect mechanism, represented by Model (1), explains the abundance of the six populations. Moreover, this explanation does not even cite the Malthus' law from which the observed population dynamics departs. The law is not sufficient for explanation since the maternal effect mechanism is required, and it is not necessary either, since the maternal effect mechanism explains the observed population dynamics. The requirement of Ginzburg and Colyvan's program to begin with the Malthus' law and then search for mechanisms to explain the departure from exponential growth unnecessarily complicates the matter.

3.2 Weber on Laws as Descriptors of Default States

Weber (1999) argues that the second explanatory role of the principle of competitive exclusion is to be part of explanations of cases to which it does not apply directly. In such explanations, the principle describes a default state, competitive exclusion, that one would expect to occur, but it does not. The description of the default state offers a contrast class for the explanation of the structure of a community. Hutchinson's work on plankton underlies this contrastive explanation. Hutchinson observed that one would expect few species of phytoplankton because it consumes few limited resources, which leads to competition and eliminates some species. However, there are many coexisting species of phytoplankton in natural conditions, contrary to what would be expected based on the principle of competitive exclusion. Faced with this situation, one could ask "Why are there many species of planktonic algae in freshwater lakes?" However, this question is difficult to answer because "one doesn't really know where to start" (Weber 1999, 83). By contrast, the question, "Why are there many species of algae, rather than just one

species: the superior competitor?” is significantly more precise (Weber 1999, 83). The principle of competitive exclusion produces a contrast class where all algae except one should go extinct. Since this does not happen, the description of a causal mechanism, which is environmental variation in the case of phytoplankton, explains coexistence by showing how algae can evade competition. In Weber’s view, the logic of this contrastive explanation is similar to explanations in classical mechanics that use Newton’s First Law, which states that in the absence of forces a body will be at rest or in uniform motion in a straight line. Considering that the body is in neither of these conditions, its motion would be explained by citing a force that removes it from rest or from the uniform motion (Weber 1999, 83).

Weber’s proposal encounters the same difficulties as Ginzburg’s and Colyvan’s view. The role of the principle of competitive exclusion as a descriptor of a contrast case, or default state is not necessary. The need to formulate explanation-seeking questions which include a contrast case is motivated by heuristic reasons. Without the contrast case, “The question is hard to answer; one doesn’t really know where to start” (Weber 1999). Arguably, not all researchers would find this difficulty insurmountable. To account for coexistence of species, they simply might look for factors that promote growth, and for the absence of factors that inhibit it. That is, one would describe a mechanism responsible for the coexistence of species. Even if the description of the contrast class is helpful heuristically to formulate an explanation, the principle of the competitive exclusion is not sufficient to answer the explanation-seeking question, since the description of a mechanism—environmental heterogeneity—is necessary.

4. Conclusion

The upshot of the foregoing examination is that the laws of ecology could figure in two types of explanations. In the first type of explanation, laws explain by direct application to the phenomenon in question, and are part of covering-law model explanations. However, I showed that models which express ecological laws could have some explanatory capacity derived from representing the mechanisms that produce regularities. Describing the mechanism is sufficient to explain the phenomenon, but citing the law is not. In the second type of explanation, the laws describe a default case that does not occur and require a description of a mechanism to explain the deviation from the default condition. My analysis revealed that the laws are not sufficient to account for the explanandum phenomenon, since the description of the mechanism is required. The laws are not necessary either because the description of the mechanism explains the phenomenon under scrutiny. Therefore, the role of laws in ecological explanations has been overstated.

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