

Struggling with the Science of Ecology

Jay Odenbaugh
Department of Philosophy
Lewis and Clark College
0615 SW Palatine Rd
Portland Oregon 97219
USA
jay@lclark.edu

A review of Gregory Cooper's *The Science of the Struggle for Existence: On the Foundations of Ecology*, Cambridge University Press (2003), 0521804329

(6,482 words)

Introduction

Greg Cooper's *The Science of the Struggle for Existence* is a must read for those interested in the history and philosophy of ecology and in topics like laws of nature, scientific explanation, and mathematical modeling. If you want to explore some of the metaphysical and methodological challenges that face ecology, there is no better place to go. Thus, this book marks an important moment in the philosophy of ecology. Folks like myself will be responding to it for quite a while.

What I find most appealing about the book is just how much there is to argue with. On every page there are interesting ideas presented but which are excitingly controversial. Some will argue with Cooper's interpretation of the history of ecology. There are parts of the book that empiricists will balk at. You will not be left unstirred. Having said this, Cooper can be longwinded and while you read you should remember patience is a virtue.

What's in a Word?

First and foremost, Cooper wants to provide an adequate definition of the science, or better yet, sciences of ecology. He writes,

Most foundational controversies involve, sooner or later, questions of disciplinary identity. It must be part of the philosophical project, therefore to say something about what ecology is. The strategy I have chosen is to defend a particular definition of ecology – the Haeckelian definition of ecology as the science that studies what Darwin calls the struggle for existence. (2003:1)

What is this struggle and who is it between? Darwin, the originator of this metaphor, writes,

I should premise that I used the Struggle for Existence in a large and metaphorical sense, including dependence of one being on another, and including (which is more important) not only the life of the individual, but success in leaving progeny. (1859: 77)

Cooper writes that the struggle for existence “...is the confrontation between the organism and its conditions of life” (2003: 4). Thus, ecology is the science that concerns the dependencies that exist between organisms and their biotic and abiotic environments recognizing that the causal action happens in both directions (Levins and Lewontin (1993), Odling-Smee et. al. (2003)).

Cooper considers several objections both to the project of defining the discipline and the definition that he has offered (2003: 6 – 16). With respect to the first issue, one can claim that any such definition will be too abstract with too little content. In ecology, there are *many, many* subfields – physiological ecology, behavioral ecology, evolutionary ecology, population ecology, community ecology, macroecology, ecosystem ecology, and landscape ecology. How can one accurately generalize over them? Moreover, any such definition will artificially constrain what counts as ecology since it is hopeless to examine *all* of these subdisciplines and abstract some set of necessary and sufficient conditions. Finally, in providing such a definition, we will simply dredge up fruitless semantic squabbles.

Cooper responds by arguing that we can “reason abstractly” about interdisciplinary space and that a definition can actually be a “tool for probing foundational inquiry” (2004: 7). In fact, his strongest reason in my judgement for hunting for such a definition is the following:

Furthermore, given the variety of associations that the term *ecology* calls to mind in contemporary intellectual (and not so intellectual culture), it is important to indicate, at least in broad outlines, the various kinds of scientific activities that have traditionally been classified as ecological. (2003: 10)

‘Ecology’ is often associated with one or more of the following three different concepts or sets of concepts: the *science* of ecology, *environmentalism*, and the *life history* of an organism, population, or community

A definition of ecology qua science will help the naïve to recognize important differences between these concepts. This is all the more important given that we live in a climate where ecologists are often thought of as products of left-wing political agendas (Chase, Fitzsimmons).

Cooper raises several objections to his account of ‘ecology’. There are four:

- The definition is biased in favor of biotic factors driving the dynamics of ecological change (2003, 13).
- “Deductive theorizing” is not paradigmatic of ecological inquiry and this biases the definition (2003: 14).
- Ecology simply is not a subdiscipline of evolutionary biology and this biases the definition (2003: 15).
- This definition ignores community ecology and ecosystem ecology – distinct levels of organization – and is “too organism centered” (2003:16).

Cooper’s definition can be defended against the first three objections. In first instance, proponents of causal efficacy of “abiotic” factors can grant Cooper’s definition without any worries since the issue is about *all* the dependencies between organisms and their environments. Likewise, the definition makes no mention of how one should study these dependencies – presumably though one should use field observation, formal theory, and bottle experiments. Thus, there is no theory bias at least in the definition. Finally, ecology need not be subsumed by evolutionary biology since we are not studying only those

dependencies that are related to expected reproductive success or constructing Darwinian histories, but once again *all* the dependencies between organisms and their environment.

My actual worry is closely related to the concern that he has artificially constrained the disciplinary space and thus to the fourth objection. On his view, ecologists study the dependencies between organisms (or groups of them) and their environments. However, ecosystem ecologists do this only in the most distant way. These “biogeochemists” are interested largely in the flow of energy and the cycling of nutrients through things like watersheds. In effect, there are no organisms in ecosystem studies unless they can be represented in terms of physical or chemical variables. Hence, Cooper’s definition is flawed.

There are two responses that Cooper could offer. First, he might claim that ecosystem ecologists are studying the *abiotic environment* of organisms and as such these studies are correlative to the more organismal areas. Second, he simply could deny that ecosystem ecology is ecology in the relevant sense. He writes at the end of the book,

I suggest a similar view of the relationship between ecosystem ecology, which might be better described as biogeochemistry, and what Hutchinson called biodemography, or what we would today call population biology. We might then distinguish between ecology in the broad and narrow sense. In the broad sense, it is the union of the individual, population, community studies – the struggle for existence in the broadest sense – on the one hand, and biogeochemistry on the other...Ecology in the narrow sense, it just is the struggle. (2003: 283)

The first response is problematic in that ecosystem ecologists do not simply study the abiotic environment *outside* the organism; rather, the organism simply *is* a transducer or conduit of energy and nutrient flow. The metaphysics of ecosystem ecology considers organisms indirectly at best in terms of ecological energetics. Second, one can take the union of ecology and any other discipline but that union need not be ecology. Cooper’s definition in my view simply leaves ecosystem ecology out of the picture. To relegate this work outside of ecology proper would be to rewrite history so that Tansley, Lindeman, the Odums, Liken,

and Boorman are marginal figures. However, a perusal of textbooks, monographs, and journals demonstrates that they are center-stage.

Of course, whether or not Cooper's account of definition of *ecology* is correct, one can profit greatly from his book because it is occupied fundamentally with some of the foremost controversies in ecology. It is to these controversies that I now turn.

The Balance of Nature – Good Poetry, Bad Science?

Ecologists have often hypothesized that there is some “balance” to populations and communities of organisms. Specifically, there are two debates that have occurred under this banner: debates over *population regulation* and the *dynamics of communities*. Cooper discusses only the former and so let me say something brief about the latter.

Community ecology has made tremendous conceptual and empirical progress with respect to *their* diversity-complexity-stability hypotheses.¹ Here is a very brief account of why. In the 1950s, Charles Elton (2000) and Robert MacArthur (1955) independently suggested a diversity-complexity-stability hypothesis. Elton provided a handful of empirical arguments for such a hypothesis involving mathematical models, bottle experiments, flora and fauna on islands, insect outbreaks in monocultures and tropical communities, and invasions on islands. These arguments were not terribly well received (see Goodman 1975 for example). MacArthur looked at the dynamics of food webs of a very simple sort and determined a measure of stability; namely, “[t]he amount of choice which the energy has in following the paths up through the food web is a measure of the stability of the community” (1955: 534). He argued that in order to maintain the species in the community, there must be a large

¹ Strictly speaking, a diversity-stability hypothesis has the following form: increasing species richness increases stability. However, a complexity-stability hypothesis involves increasing variables other than simply the number of species.

number of paths in the food web. This was important work in moving thought about a balance of nature from natural history to ecology.

However, the floor dropped out on the community diversity-complexity-stability hypothesis in the 1970s with the appearance of the ex-particle physicist Robert May. Using local stability analyses, he demonstrated that small perturbations to systems of differential equations describing species abundances around their equilibrium would take them away from this equilibrium. Thus, increasing the complexity of a community – the number of species, the number of interactions, or intensity of those interactions – decreases its local asymptotic stability. Fortunately, ecologists such as C. S. “Buzz” Holling (1973), Gordon Orians (1975), and Stuart Pimm (1985) recognized that actually there are *many* different *diversity*, *complexity*, and *stability* concepts at issue, which leads to a *large* number of possible hypotheses. Hence, the complexity-stability hypotheses are not dead and given the work of individuals like David Tilman and Shahid Naeem, some of them have been highly confirmed. For example, Tilman has been by conducting large-scale experiments at Cedar Creek Natural History Area in Minnesota. These experiments have shown that species richness is positively correlated with plant community stability – there is a decreased coefficient of variability of plant community biomass with increasing numbers of species with little effect on the variability of the component populations (hence the irrelevance of May’s result). There is still much controversy over whether increasing diversity causes or is merely correlated with decreasing plant biomass variability.

Thus, in community ecology, we see conceptual refinement, empirical testing, and theoretical modeling working together. Whatever may be true about the balance of nature debates in population ecology, from a methodological point of view things are looking very

good in community ecology. Thus, I would argue that with respect to community ecology, it is incorrect to write as Cooper does,

[The balance of nature idea] usually functions as a background assumption that is rarely brought forward for explicit study. This remains largely true of the balance of nature idea in ecology as a self-conscious scientific field; it has worked in the background, shaping inquiry, but it has rarely been hauled out into the daylight and closely examined. (2003: 75)

That said, Cooper suggests things have not been going well in population ecology.

Population ecologists have been arguing for quite some time over whether or not populations are *regulated*. It is a fact of nature that many populations persist through time. Technically, many a population's abundance has a mean value with only a moderate amount of variance around that mean. The *biotic school* was developed by Howard and Fiske (1911), A. J. Nicholson (1933), and Frederick E. Smith (1935) and they contended that populations are regulated – they are *caused* to vary around that mean – primarily by factors that depend on their density. There are mechanisms present in populations such that they will increase when low and will decrease when high and thus average population densities remain stationary. The *climatic school* pioneered by Bodenheimer (1931) and most forcefully by Andrewartha and Birch (1954) argued that populations are driven by changes in the abiotic environment like weather and thus fluctuate greatly. Generally speaking, on their view the abiotic environment is not hospitable enough for density-dependence to kick in since population abundance is kept sufficiently low.

Cooper argues that these two camps and their descendants have largely presented their case on *a priori* grounds. He presents the arguments (“inferential tendencies”) for a balance of nature concerning population regulation in two forms. Here is the first.

Balance of Nature Argument I

1. The relative constancy of population sizes, given what the capacity for increase would allow, implies that populations are regulated.

2. Since this order, in the face of a fluctuating abiotic world, is the product of evolution by natural selection, the forces that achieve it must themselves be under evolutionary control – that is, they must be biotic forces.
3. When these biotic forces are unimpeded by noise from the abiotic environment and the vagaries of history, they should issue in equilibrium populations.
4. Effective regulatory control presupposes sensitivity to changes in population density – we should expect these biotic factors to be density independent.
5. Competition is the most likely mechanism for the implementation of these controls.

Now this argument is problematic for all sorts of reasons.

First, even if populations have a relatively constant abundance it does not follow that there is a stable equilibrium they are varying around. The range of variation of this variation itself is significant depending on the taxon of choice since Lack's birds are not Andrewartha's insects. Second, if by "relatively constant" we are allowing for a large amount of variation around that mean, then populations can persist and not be regulated by density-dependent mechanisms. Cooper argues with others that metapopulation theory provides one such place to look (2003: 17, 86). In the simplest model, imagine you have a set of homogeneous patches, each of which can be occupied by one and only one population. Let p_i be the probability of local colonization, p_e be the probability of local extinction, and f be the fraction of patches occupied. Thus, we have the following differential equation.

$$\frac{df}{dt} = p_i(1-f) - p_e f$$

If $df/dt = 0$, then the stable equilibrium is given by

$$\hat{f} = p_i / (p_i + p_e)$$

Depending on the parameter values,

Persistence of the overall population – the metapopulation – might be a consequence of the pattern of extinctions and successful migrations among the subpopulations, *even though* the latter are governed in a density-independent fashion. (2003: 86)²

² We should note that metapopulation models of the sort mentioned presuppose the existence of stable equilibria. Thus, there still is a balance of nature here, albeit a different one from the one under consideration.

Finally, suppose that there is a stable equilibrium for a given population and there are density-dependent mechanisms regulating the population, it does not follow that the mechanism must be intraspecific or interspecific competition. My favorite alternative mechanism is *apparent competition*. If a predator species preys on two resource species in a way that depends on which resource species is most common, then the population can have an equilibrium density regulated by a density-dependent factor, the choosy predator. Thus, the argument as it stands is deeply flawed.

Cooper goes on to present a more recent version of this argument which goes as follows (2003: 87).

Balance of Nature Argument II

1. Persistence is an ecological fact – the populations are here.
2. Since unregulated populations are statistically destined to random walk their way to extinction, most populations must be regulated (in the *SPD* sense).
3. Since being regulated *just is* having an equilibrium, most populations are under the influence of density-dependent factors.
4. Furthermore, since regulation implies density dependence, most populations are under the influence of density-dependent factors.
5. Finally, since biotic forces are the most likely mechanisms for density dependence, we should expect biotic forces to be important determinants of population behavior.

In many respects, this argument proceeds as the other did except it has more fancy terminology like Peter Turchin's *stationary probability distribution (SPD)*.³ However, where the previous argument simply assumes empirical claims with no evidence; in addition, this argument *defines away* many of the empirical issues. First, a population is said to have an equilibrium just in case it is regulated. Second, a population is said to be regulated just in case it exhibits density-dependence. Thus, a population is said to have an equilibrium just in case it exhibits density-dependence. Scientific progress made easy.

³ A time series of data exhibits a *stationary probability distribution* if there is a mean density about which the population density fluctuates and where the variance around the mean is bounded in the long term.

I have no doubts that some ecologists have been guided by unjustified presuppositions and some have been very sloppy with these concepts. However, once we distinguish the worries about the *a priori* of the population regulation debate, I think things will look more promising. Let us distinguish between two ways in which the debate over population regulation can go astray. First, the debate can go astray when the evidence is ignored and one simply tosses around judgments of plausibility. Second, one can define one's terms such that putatively empirical issues are settled by definitions. However, ecologists have been much more sensitive to evidence than Cooper suggests and one can straightforwardly characterize the concepts involved so that the issues can be answered in an empirical manner. Let me discuss the second issue first.

Consider the following questions. Do populations have a mean population abundance around which there is only a moderate amount of variation? This is a statistical question. For those populations for which the answer is yes, is there a causal mechanism which causes it to vary around that mean as a function of population abundance? This is a causal question. For those populations for which the answer is yes, is this caused by competition between conspecifics? Here we have the right sort of logical independence and each of the questions can be subjected to empirical evidence. Thus, if some ecologists define their concepts sloppily, they need not do so. Now let's move on to the first issue of empirical evidence.

In 1948, J. Davidson and Andrewartha published a study on *Thrips imaginis*, a plant-sucking insect, which lived in roses grown at the Waite Institute in Adelaide, Australia. They counted the number of *Thrips* in a sample of twenty roses every week for fourteen years. Each year the number of *Thrips* reached a peak value towards the end of the month of November (figure 1).

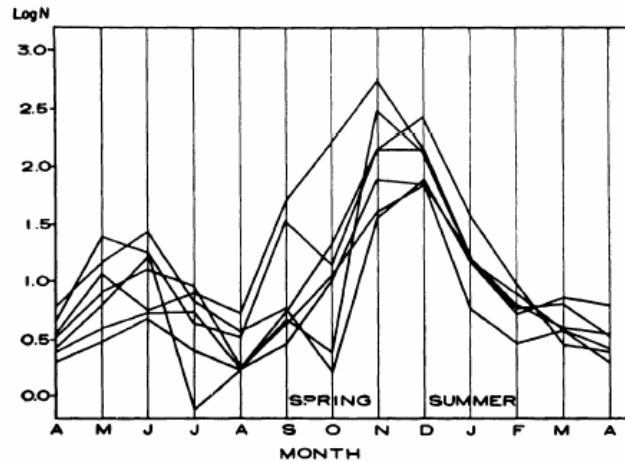


Figure 1. The logarithm of the average population size per month for several years in the study of *Thrips imaginis* (1961, 404)

Davidson and Andrewartha attempted to determine the effect of weather on population abundance by finding correlations with meteorological factors using multiple regression. In Adelaide, the winters are cool and rainy and the summers are hot and dry. Thus, ignoring much detail, the *Thrips* do better in the summer and only in the winter months do they reach the peak and then quickly decline. Davidson and Andrewartha's equation took the usual linear following form, $Y = b_0 + b_1X_1 + b_2X_2 + b_3X_3 + \dots + b_nX_n$. The independent variables of the model were

- X_1 = the number of day degrees up to the 31st of August,
- X_2 = day degrees in September and October,
- X_3 = day degrees in August of the previous season, and
- X_4 = the rainfall in September and October

The dependent variable Y is the average of the logarithm of *Thrips* per flower over the thirty days before the population peak. The independent variables of the model "captured" 78% of the variance. Davidson and Andrewartha concluded first that *Thrips* consumed very little of the available food and second that the variation in abundances were accurately captured by variation in weather. Thus, Andrewartha and Birch (1954) wrote, "...not only did we fail to find a 'density-dependent factor,' but we also showed that there was no room for one".

Frederick E. Smith (1961) argued that their analysis simply *could not have* revealed density-dependence in *Thrips* and a proper analysis:

...supports the thesis of strong density-dependence in this population, and furthermore that the analytic model of Davis and Andrewartha is not appropriate to their theoretical interpretation, and is in fact appropriate to the concept of density-dependence. (1961: 403)

First, Smith noted to detect density-dependence we must examine *relative* not simply *absolute* population abundance (1961: 403). By estimating the rate of population change from average logarithms $\overline{\Delta \log N}$ and population size $\log N$, he found that they were negatively correlated immediately preceding the spring peak (1961: 404). If density-dependence was occurring in the populations, then the rate of population change should be negatively correlated with population size. Second, Smith noted that if density-independence was truly alone, then the variance of the logarithm of average population size $\log \bar{N}$ should increase with population size (figure 2).

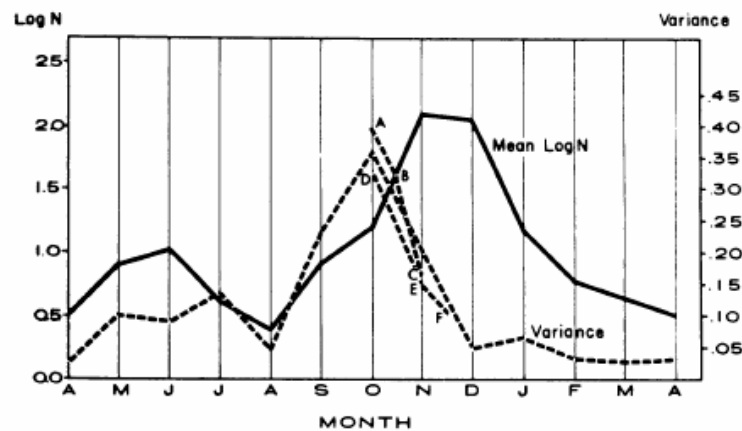


Figure 2. The variance of the logarithm of the average population size each month along with the average curve of population size (1981, 406).

However, we see the variance of $\log \bar{N}$ decreases as $\log \bar{N}$ increases in the months of October, November, and December (1961: 406).

My point here is not to suggest that Smith got the best of Davidson and Andrewartha but rather to suggest that much of the debate over population regulation occurred and occurs over empirical facts. As Smith recognizes, showing density-dependence in Davis and Andrewartha's *Thrips* data was extremely important; and even strategic since "[t]he data in the thrips study are among the most detailed and comprehensive that are published for a field population" (1961: 403). Thus, ecologists have been bringing the balance of nature out from the background and exposing it to test. If one surveys the debates too abstractly, then there may be many unconvincing arguments flying back and forth. However, when one examines the issues on the ground, we see something other than intuition swapping.

Laws, Explanation, and Models – a Troubling Triad

Ecological laws are hard to find if by 'law' we mean a statement "...involving spatiotemporal generality, purely qualitative predicates, and the like..." (2003: 177). This is not to say there are no ecological generalizations for they abound. Cooper argues there are three sorts: *phenomenological generalizations*, *causal generalizations*, and *theoretical principles*. Let me give examples of each.

As an example of a phenomenological generalization consider the species-area relation. Ecologists have long recognized that as area increases, so does the number of species in that area. The biogeographer Phillip Darlington surmised that with every tenfold increase in area, the number of species doubles. One species-area model that fits many data sets is the power function

$$S = cA^z$$

where c is a fitted constant and z is a parameter that has values in the range 0.15 and 0.35.

The value z takes depends on several factors. Most significantly, species that have small

geographical distributions have higher α -values and species with larger geographical distributions have lower α -values.

As a causal generalization, we can consider the work of Robert Paine and his colleagues. Paine has conducted much of his research in marine intertidal zones along the coast of Washington state studying the predator starfish *Pisaster* and its mussel prey *Mytilus*. When *Pisaster* was removed, *Mytilus* began to competitively exclude other species in the area thus reducing intertidal the diversity. Hence, one causal generalization one can draw from this work is “...*Pisaster* is a significant factor in maintaining species diversity in the marine intertidal zone along that stretch of coastline” (2003: 109). More generally, Paine and his coworkers suggested the *intermediate disturbance principle*; namely “...that a certain level of disruption, such as the removal of individuals by predation, is an in important determinant in species diversity in marine intertidal communities” (2003: 110).

Finally, as an example of a theoretical principle, consider a principle from the theory of limiting similarity. Consider a unidimensional resource distributed continuously on which there are three species. Each species has it own mean position d on the spectrum with a variance w around this mean described by a resource utilization distribution (Figure 3).

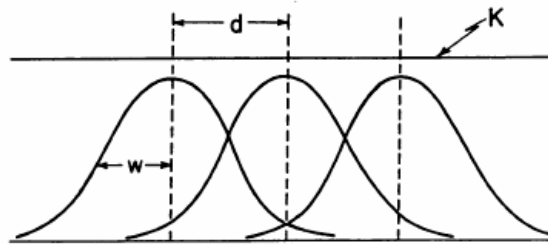


Figure 3. The curve labeled K represents some resource spectrum which contains three species whose resource utilization function is characterized by a mean d and standard deviation w (May 1973: 140).

The resource spectra might be food size or food at different heights in a forest. We can thus understand niche overlap as the ratio d/w . Theoreticians have been interested in determining how much niche overlap is compatible with stable coexistence of species. Given the usual assumptions of the Lotka-Volterra competition equations, that there are only three species, the resource utilization distributions have exactly the same shape but differ only in position, and the carrying capacities of the species are similar, Richard Levins and Robert MacArthur (1967) and Robert May (1973), demonstrated that competing species could coexist only if the niche overlap $d/w \approx 1$. If the $d/w > 1$, then there are underexploited resources and intraspecific competition will increase niche overlap. On the other hand, if $d/w < 1$, then conditions for coexistence are very stringent given the niche overlap and thus interspecific competition will push the niches apart. Thus, limiting similarity, the minimum distance between the means of the curves, should be such that $d/w \approx 1$.

The fact that there are few if any laws in ecology creates a big problem when it comes to explanation since we must face a trilemma:

1. There are no laws in ecology.
2. There are genuine theoretical explanations in ecology.
3. If there are genuine theoretical explanations in ecology, then there must be ecological laws.

If you concede there are no laws, then must you also concede there are no theoretical explanations in ecology either? There are several escape routes that one can consider:

1. Defend the view that ecology has laws suitably construed; for example, they are generalizations with possibly vague *ceteris paribus* clauses.
2. Deny that ecology has genuine (read “objective”) explanations since they are essentially pragmatic.
3. Deny the conception between explanation and laws – one can have objective explanations without them.

Cooper essentially agrees with (3) and thus let me explain why the other two options are problematic in his view.

Suppose we construe ecological laws as true generalizations with *ceteris paribus* clauses. If we do, we must recognize that we have very few laws on the books. The *ceteris paribus* clauses can almost never be written down, we have next to no evidence that we could use them, and this would not necessarily solve all the problems since law are supposed to be necessarily true, universal, and support counterfactuals (2003: 180). Thus, Cooper considers this and other strategies implausible.

One could also be an instrumentalist like ecologist R. H. Peters and simply deny that “explanatory potential is an independent dimension of virtue for scientific theories”; specifically, a *cognitive* as opposed to *pragmatic* virtue (2003: 184). The fundamental aim of science is predictive success and nothing more. Cooper offers two replies to the instrumentalist (2003: 185). First, if we take predictive utility as the sole measure of success, then this will “spell disaster” for ecology given this is what it lacks. Second, it would also follow that the theoretical tradition of model building would be extremely overvalued in ecology and he believe it has “cognitive payoff” as we shall see. I think that the instrumentalist or pragmatist but more on that below.

So, Cooper rejects (3) – ecology can provide objective explanations without possessing laws. He claims that need a better account of explanation and of the generalizations that play a role in such an account. Let’s first consider ecological generalizations.

Any account of ecological generalizations, which are explanatory and yet are not laws, should meet the following criteria (2003: 97):

- They must possess “nomic force” which itself is a matter of degree,
- The generalizations can have limited scope varying over space, time, taxa, and trophic level, and
- Theoretical principles can be explanatory when they express our “fundamental commitments”.

In order to provide the needed account, Cooper employs the analytic machinery of *resiliency*. Suppose you have a statement q and set of logically independent statements $p_1, p_2, p_3, \dots, p_n$. If we further suppose that $\Pr(q) = n$, then we have the following measure of resiliency:

$$\text{Res}[\Pr(q) = n] = 1 - \max_i |n - \Pr(q/p_i)|$$

where p_i ranges over all combinations of p s. What this measure does is compare the probability of q with the probability of q conditional on the p s. Consider the extreme cases. Suppose that q and p s are probabilistically independent. Then $\Pr(q) = \Pr(q/p_i)$ are thus $\text{Res}[\Pr(q) = n] = 1$. On the other hand, suppose the p s entail q . Then $\Pr(q/p_i) = 1$. Hence, $\text{Res}[\Pr(q) = n] = 0$. Resiliency then can be thought of as a measure of the stability of a generalization over different possibilities.

Now as a scientific community, ecologists cannot consider every logically possible p , and thus they must constrain these claims in some way. Cooper argues that the possibilities are constrained by virtue of disciplinary background knowledge and fundamental commitments (2003: 118-9). Formally, one can think of this as providing a weighting w_i for each p_i .

As a piece of analytic machinery, resiliency is perfectly respectable. However, I have grave doubts whether it can be of much use since it requires us to assign unconditional and conditional probability values to ecological generalizations. There are essentially three interpretations that they can be given: limiting frequency, propensity, or subjective interpretations. If we give them a limiting frequency interpretation, then we must determine the truth-value of the generalization in a number of replicates or scenarios and conditional on many, many other propositions as $n \rightarrow \infty$, which seems extraordinarily difficult. If we give a propensity interpretation, then we must determine the disposition of a generalization's

being true and being true conditional on others; it is not clear what this means nor how we could determine it. If we give a subjective interpretation, resiliency becomes a subjective affair, which I believe would be anathema to Cooper's overall project. Thus, though I completely concur that ecological generalizations have "nomic force", I do not think resiliency provides an analysis of the notion.

Cooper uses the work of Jim Woodward to develop his theory of explanation which remarkably combines both causal and unificationist elements. The fundamental notion is that of *counterfactual invariance* where invariance comes in degrees. There are two types of invariant counterfactuals of interest – *active* and *passive*. An *actively invariant counterfactual* is a statement of the form "if *X* were intervened upon, then *Y* would result" subject to technical requirements (2003: 210). A *passively invariant counterfactual* is a statement of the form "if *X* were the case, the *Y* would result" for which we have no "...understanding of what it would take to realize the antecedent of the counterfactual" (2003: 207). On Cooper's view, invariance is what makes for a "nominally strong generalization" – it has high resiliency over a "counterfactual domain" (2003: 209). So, on his view then, causal generalizations are invariant (resilient) over active domains and phenomenological generalizations are invariant (resilient) over passive domains.

We can now see how Cooper weds the two "venerable intuitions" of causal and unificationist accounts of explanation. First, invariant generalizations can be claims about functional or supervenient properties. Moreover, these invariant generalizations about such properties may not be causal; nonetheless, they can be explanatory when they "...effect significant systematization of phenomena" (2003: 216). Thus, even if the invariant domain is sufficiently large, then we can have explanation without causation. This then provides us with an *explanatory continuum* where the invariant generalizations are active which grades into

invariant generalizations that are passive. However, Cooper does believe with a nod to Richard Levins that "...a gain in one virtue is invariably accompanied by sacrificing the other" (2003: 219) though this is not necessary for his account.

So, a causal generalization explains some phenomena by demonstrating that is a part of an invariant active domain it describes and a phenomenological generalization explains some phenomena by demonstrating that it is a part of some systematic invariant passive domain it describes. However, this leaves us with the last category – that of theoretical principles. How are they explanatory? Consider the following:

[I]f we look at the explanatory practices of theoretical ecology and at what the ecologists have to say about their own efforts, there is reason to wonder if nomically strong generalizations might not meet the same fate as laws – there are not enough of them to go around. (2003: 220)

The problem here is the claim that there are instances of theoretical explanation – model-based explanations – for which there is no corresponding nomically strong generalization. For to determine if a model captures a nomically strong generalization, we need to determine whether the model bears a sufficient goodness-of-fit to phenomena or that the assumptions of the model are approximately true of the phenomena (2003: 220). However, given the problem of predictive accuracy, there will a large number of models and claims derived from them for which this is not true. So, Cooper argues in the following way:

If we are looking for generalizations that might underwrite the explanatory power of theoretical models, then we should be looking not for *empirical* generalizations but for *theoretical* generalizations. The latter talk about how ecological systems are *disposed* to behave (2003: 21).

To put this in perspective, we can see how the species-area relation might explain as an invariant generalization since it is systematically true over a passive domain. Similarly, the intermediate disturbance principle might explain as an invariant generalization over an active domain. However, what about the $d/w \approx 1$ rule and its co-conspirators? How can theoretical

principles like it be explanatory? Following the lead of Nancy Cartwright, Cooper argues that models that do not have corresponding nomically strong generalizations can be explanatory provided that they express an abstract *capacity* or *tendency*.

Consider the theoretical principle that “simple difference equations yield complex dynamics” (2003: 222). In the 1970s, Robert May (1976) demonstrated that simple discrete difference equations could exhibit chaos understood as dynamical behavior which is extremely sensitive to initial conditions and which is unstable and aperiodic. Thus, using the following equation:

$$N_{t+1} = N_t + R_t N_t (1 - N_t / K)$$

he determined if the per capita rate of increase $R \leq 2.57$, then the model exhibited stable equilibria and stable cycles. However, if $R > 2.57$, then chaos would occur. Now the problem with models that exhibit chaos is both their simplicity and complexity. If the model is extremely idealized which they invariably are, then we can be sure that *no* empirical system will satisfy its assumptions. Similarly, given sensitivity to initial conditions and the unavoidability of measurement error that blows up exponentially, we cannot accurately predict the evolution of our system through time.

On Cooper’s view then, good models are usually formal structures which describe capacities or tendencies and they “...can be important because [they] reveal new and unanticipated dispositions in the phenomena” (2003: 233). This however leads us to the fundamental question: why should we accept those models as explanatory when they have not been tested by ascertaining either the approximate truth of their assumptions or goodness-of-fit? Since Cooper *already believes* they are explanatory, he introduces the Cartwrightian stratagem that they represent abstract capacities and tendencies in order to

preserve their explanatory power in light of their distance from empirical phenomena. However, this strikes me as putting the proverbial cart before the horse.

For every ecological model, does there correspond a capacity or tendency? Cooper would say no because not every model expresses our deepest “theoretical commitments”. However, though this would allow us to separate $d/w \approx 1$ from ecological chaos, this still leaves us with *massive* underdetermination problems. By hypothesis, you cannot test these models in the usual sense mentioned above, so how can he claim:

...the fundamental role of our knowledge of abstract tendencies and capacities is to give us information about what is possible for the phenomena we want to give us information about what is possible for the phenomena we want to understand. (2003: 247)

That is, how can one *know*, or even be justified in believing, that the model “reveals new and unanticipated dispositions in the phenomena”? This problem becomes even more apparent when we consider the fact that often there are a large number of distinct models representing a common phenomenon via a set of dependent variables. If none of these models can be tested against the phenomena of interest, then it seems that we simply cannot say what dispositions the phenomena have. Thus, I suggest that when model cannot be tested, we have no reason to suggest that it is explanatory. Explanation simply cannot be this liberal.

Now, I do grant that chaotic and the limiting similarity models we discussed do perform valuable functions in ecology. However, this is just the sort of story that the “theories as tools” approach Cooper discusses at length would have us expect (2003: 155 – 71). For example, the limiting similarity models were a natural follow up in investigating the competitive exclusion principle which said that when two specie have identical niches they cannot coexist. Of course, species never have *exactly* the same niches and thus the principle is

trivially true. So, how much niche overlap can occur given shared resource use? That work was designed to answer those sorts of questions (subject to an *enormous* number of qualifications I have not discussed). Chaotic models as explored by May are extremely important not only for awaking us to the possibility of ecological chaos but also for challenging the fundamental assumptions in debates over population regulation. As May writes,

These studies of the Logistic Map revolutionized ecologists' understanding of the fluctuations of animal populations... With the insights of the Logistic Map, it was clear that the Nicholson-Birch controversy was misconceived. Both parties missed the point: population-density effects can, if sufficiently strong..., look identical to the effect of external disturbances. It's not a question of either/or. (May 2002, 39-40).

I believe that one can take the insights of Cooper's approach into a more "enlightened" empiricism or what I prefer to call "pragmatism". First, we recognize that the fundamental aims of science are anticipation of and intervention in the natural world. Thus, predictive accuracy is a necessary (and possibly instrumental) aim of science (as is truth); however, often models must perform heuristic roles in pursuit of this aim and rarely will be immediately tested. Thus, they are valuable in developing testable theory even when they are not predictively accurate or explanatory. Second, as causal realists, we can accept that explanation occurs by subsuming events under nomically strong generalizations in the way that Cooper suggests whether we are talking about active or passive domains. Third, given that models often provide us with "untestable tools", we can grant their usefulness without having to accept them as explanatory given that they do not have the appropriate evidential credentials. Thus, as pragmatists, we can leave behind commitments to abstracta like capacities and tendencies.

Conclusion

With important exceptions notwithstanding, ecology has been largely ignored by philosophers of biology (though not by historians). Cooper's book will I believe help remedy this situation. It is a great resource for struggling with the fascinating controversies in ecology and is thankfully controversial itself.

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