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INTRODUCTION: UNDEAD DOGMAS OF EMPIRICISM

> I suspect the demand for evidence about individuals is a
> bastardized version of an old positivist claim: the claim
> that theoretical terms must be defined in observational
> ones, in particular individual sensory experiences.
>
> Kincaid 1996, 182

The philosophy of biology has matured quite a bit over the last two decades. Back in 1988, Ruse noted a conspicuous dearth of work on ecology. But by 1999, Sterelny and Griffiths devoted an entire chapter to it in their introduction to the philosophy of biology. There is still plenty of room, and reason, for more philosophical attention to a science so vital for understanding and addressing environmental concerns. But at least several people now make philosophy of ecology their academic specialty.

In the following I shall very briefly survey recent developments in both ecology and the philosophy thereof. One important aspect of the developments within ecology is an expansion to larger spatio-temporal scales of investigation. This wider focus has often, though not always, resulted in a shift in perspective, from viewing ecological entities as closed systems to treating them as open systems. I will take a closer look at three examples of scale expansion and tease out some of their implications for environmental policy, on one hand, and still-common reductionist philosophies of science, on the other. Finally, I will consider the philosophical implications of the search for mechanisms, when the open nature of the systems under study is acknowledged.

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But first, some wider context. In the early twentieth century, the logical positivists espoused a certain kind of ethical subjectivism, a certain kind of reductionism, and a certain kind of instrumentalism. Respectively, these doctrines held that ethical statements are meaningless emotional outbursts, that theoretical predicates are reducible to observational predicates, and that questions about the truth or falsity of statements regarding ''unobservable'' entities are also meaningless. Most philosophers have since rejected all three of these positions. But other versions of subjectivism, reductionism, and instrumentalism persist within both philosophy and science.

By the end of the twentieth century, scientific realism had arguably eclipsed instrumentalism within philosophy of science. Nevertheless, new versions of instrumentalism still crop up. One might think that a field like ecology should be largely immune to the whole debate. The entities that it deals with are mostly ''observable'', and hence not subject to the skepticism traditionally leveled by instrumentalists against ''unobservable'' objects like atoms. Yet Sober has argued for instrumentalism regarding hypotheses about the degree to which the corn plants in two fields differ in average height (Sober 1999). I have shown that even in the new ''Akaikean'' statistical framework invoked by Sober, theories achieve predictive accuracy in the way that realists say they do. Predictive success results from getting at the underlying truth – not from the kind of ''cosmic accident'' required by instrumentalist accounts (Mikkelson in press).

It may be that most philosophers of science now consider themselves to be antireductionists. And yet most arguments against reductionism attack only an extreme version of it: the idea that lower-level processes *completely* explain higher-level processes (but not vice versa). I submit that it is time also to question a slightly milder version of reductionism that seems to guide scientific funding policy, as well as many scientists' views about proper methodology. According to this type of reductionism, lower levels ''merely'' play a far more important role than higher levels, in explanations of most phenomena. For example, scientific funding patterns imply that genetic causes of human disease are far more important than environmental causes. In the following, I shall offer some reason to doubt this kind of position, at least within ecology.

The debate over ethical subjectivism versus ethical realism has not attracted much comment in philosophy of biology (Sober 2000 is

an exception). And yet this debate has profound implications for the question of whether science can or should be "value-free" (Putnam 2002). In the following, I shall limit my remarks to noting some of the policy implications of recent research on the causes and consequences of biodiversity.

1.   A VERY BRIEF SKETCH OF RECENT ECOLOGY AND PHILOSOPHY THEREOF

Beatty cited four sets of "interesting foundational and methodological problems" in ecology (Beatty 1998):

1. "[P]roblems of clarifying the differences and causal connections between the various levels of the ecological hierarchy (organism, population, community, ecosystem)"
2. The "issue of how central evolutionary biology is to ecology"
3. "[L]ong-standing issues concerning the extent to which the domain of ecology is more law-governed or more a matter of historical contingency" and
4. The "related question of whether ecologists should rely more on laboratory/manipulative versus field/comparative methods of investigation."

Since Beatty published his overview, ecologists have discovered numerous interlevel causal links and other lawlike generalizations (cf. 1 and 3; see, e.g., Kinsey 2002, Marquet et al. 2005). Some progress has also occurred with regard to at least one aspect of the relationship between ecology and evolution, namely, the extent to which entire ecological communities or ecosystems are targets of natural selection (see 2; Swenson, Wilson, and Elias 2000). And "laboratory/manipulative" and "field/comparative" research programs have both continued to proceed with vigor (4). Nor do I know of any major shifts in emphasis between the two.

Since 1998 philosophers, and scientists offering philosophical commentary, have paid the most attention to the third topic; namely, laws in ecology (Cooper 1998, Colyvan and Ginzburg 2003, Mikkelson 2003). Severe ambiguity about what laws are still plagues this body of writings, just as it dogs more general discussions of laws in philosophy of science. Partly for this reason, I shall herein

avoid the question of lawhood in general and focus instead on other aspects of particular ecological "laws". Some work has been done on the first two topics, though. In Sections 2 and 3, I offer new examples and arguments regarding the issue of links between levels of ecological organization. As for the relationship between ecology and evolution, philosophers of biology have tended unfortunately to depict the former as a handmaiden of the latter (Sterelny and Griffiths 1999).

I am not aware of any sustained philosophical discussions since 1998 of Beatty's fourth topic, different empirical approaches in ecology. His dichotomy of "laboratory/manipulative" versus "field/observational" obscures important aspects of this subject, though. For one thing, many of ecology's most important advances have resulted from manipulative field experiments (e.g., those of Paine 1966, Simberloff and Wilson 1969, Likens et al. 1970; see Diamond 1986 for a general discussion, and Section 2c for another example). And yet such experiments straddle Beatty's two categories, rather than fitting neatly into either of them.

For another thing, the relative prominence of different empirical techniques seems to be a less crucial methodological issue than the degree of integration among theory, experiment, and observation. As in any field, these three modes of ecological research are sometimes tightly coupled, and at other times fairly insulated from each other. Intuition as well as a cursory historical survey of science in general and ecology in particular, suggest that better integration yields more substantial scientific progress. The example discussed in Section 2a nicely illustrates the benefits resulting from improved integration of theory, experiment, and observation.

Before proceeding further, I should mention at least a few other cases of recent philosophical work on ecology. Odenbaugh (2001) dealt with philosophical issues stemming from a period of strident reductionism, particularism, and pessimism in ecology (from the late 1970s through the 1980s). De Laplante (2004) has considered relationships between ecology and the social sciences. And environmental ethicists have continued to write about ecological science, as they have for several decades. In some cases, these efforts have yielded astute analyses of ecology resulting from long and deep reflection on the nature of this science and its moral implications (cf. Skipper et al. in press).

2.   GOING MACRO

The common theme uniting the three case studies considered in this section is a shift toward larger scales. Historically, ecologists concentrated on the internal dynamics of local populations, communities, and ecosystems. Now they more often also take into account, or turn their focus toward, the larger wholes that contain local ecological systems. These include metapopulations, metacommunities, landscapes, regions, biotic provinces, and, at the largest scale to date, the entire biosphere or ecosphere. In many cases, such a change in focus has resulted in promising new insights. In this section, I shall assess the philosophical significance of expanded spatiotemporal perspectives on relationships between (a) plants and herbivores, (b) area and number of species, and (c) number of species and the total density of biomass summed across all species.

a.   Responses of Different Trophic Levels to Nutrient Enrichment

Leibold and colleagues noted a striking mismatch between certain manipulative experiments, including field experiments, along with theoretical models, on one hand, and observational surveys of unmanipulated ecological systems, on the other (Leibold et al. 1997). The theory, experiment, and observation in question all focused on changes in plant and herbivore biomass density[1] due to increases in the nutrients that plants need to grow.[2] Most of the ''nutrient enrichment'' experiments surveyed by Leibold and colleagues fit one of two patterns: as nutrient levels increased, either plants increased proportionally much faster than herbivores, or vice versa.

These experimental results fit nicely with the predictions of some simple theoretical models. According to such models, if the plant species in question are all relatively edible, then increasing the nutrient supply does not increase total plant density very much. Instead, herbivores ''chow down'' on most of the ''extra'' plant production, leading to a proportionally much greater increase in their own density. I loosely follow Leibold in calling this scenario a closed ''food chain'' (Leibold 1996). See the steepest line in Figure 20.1.[3]

Similar models predicted that if some of the plants are relatively inedible, nutrient enrichment should increase their density
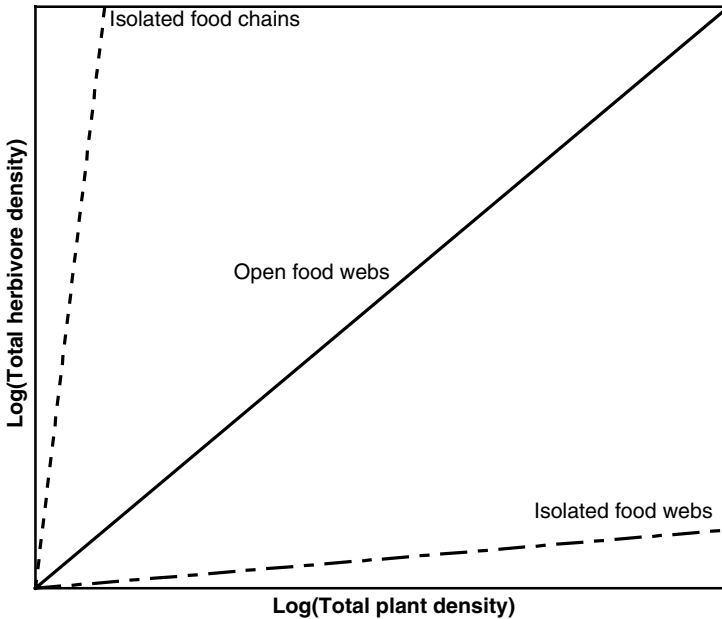
Figure 20.1 Schematic depiction of contrasting relationships between the responses of plants and herbivores to nutrient enrichment

substantially. This is because the inedible plants do not suffer as much chowing down. This relative immunity gives them a competitive advantage against more edible plants. And this, in turn, leaves the herbivores with relatively less to eat. So the herbivores increase little, if at all, in density with increased nutrient levels. This is the ''closed food web'' scenario[4] (cf. the shallowest line in Figure 20.1).

The nutrient addition experiments and theoretical models described contrast markedly with observations of unmanipulated natural ecosystems. Among these systems, plant and herbivore densities both increase significantly with nutrient levels, as depicted by the middle line in Figure 20.1. A shift in spatial and temporal perspective enabled Leibold and associates to reconcile these observations with theory and experiment. They noted that the theoretical and experimental models at hand both treated ecosystems as if they were isolated from their surrounding landscapes or regions. Consequently, these models did not allow for the colonization of new species from outside a given ecosystem.

Theoretical models that take colonization into account predict significant increases of both plant and herbivore density with nutrient levels (an "open food web" scenario).[5] To understand this, consider that relatively inedible plants generally require greater amounts of nutrients than do more edible species. This is because resistance to herbivory, for example, through the production of noxious chemicals, can be physiologically taxing. Nutrient enrichment therefore allows progressively more inedible species to colonize. Colonization by more inedible species, in turn, increases overall plant density and reduces herbivore density, relative to the food-chain scenario. In Figure 20.1, a tilt downward from the steepest line would represent this outcome.

This raises the question of whether colonization by inedible species should cause herbivore density to decline so dramatically that it results in the same pattern found in the isolated food web scenario. The reasons given by Leibold and associates that this does *not* happen are somewhat obscure. It would suffice, however, for nutrient enrichment to permit the colonization of herbivore species with the ability to overcome the defenses of the "inedible" plants. Overcoming plant defenses can also be physiologically taxing. Therefore, herbivores able to do it stand a better chance in the presence of higher nutrient levels, and thus greater overall plant production. Colonization by this kind of herbivore would result in a tilt upward from the shallowest line in Figure 20.1.

Just as in these theoretical models of open ecosystems, experimental models that allow new species to colonize from outside the ecosystem result in roughly proportional increases in plant and herbivore density with nutrient levels. One methodological take-home message is that models treating local ecosystems as open systems accord with observed patterns in nature. Theories and experiments that treat such ecosystems as though they were closed do not fit these observations.

This take-home message potentially undermines the type of reductionism discussed in Section 3. According to that doctrine, the parts of an entity should play a much more important role than its environment in explanations of that entity's behavior. Since a closed system, by assumption, has *no* environment – no larger system that could exert *any* material influence – treating an entity as a closed system takes this reductionist prescription to an extreme degree. But

an open-system approach leaves open the possibility that the environment plays an equally, or even more, critical explanatory role than the parts.

Some reductionists have rationalized their position by claiming that reduction is "the only method of attaining unitary science that appears to be seriously available" (Oppenheim and Putnam 1958). Some antireductionists concede the idea that reduction is the only viable route to the unity of science (e.g., Dupré 1993). Yet tracing causal influences both "upward" from the parts and "downward" from the environment offers more chances to unify our understanding of different levels of organization than would limiting attention to internal dynamics alone.

b.   Species-Area Relations

As in the plant-herbivore studies outlined previously, ecologists have also recently expanded the spatial scale at which they investigate relationships between area and number of species. The "species-area relation", or "law", is one of the most venerable patterns in ecology. At least in part because of practical constraints, ecologists historically began exploring species-area relations among relatively small patches of habitat. These patches generally fell into one of two categories – either contiguous parts of larger habitats or islands. However, Rosenzweig has issued a bold new claim about species-area patterns among entire "biotic provinces" (Rosenzweig 1995).

Strictly speaking, Rosenzweig did not distinguish contiguous patches from islands from provinces on the basis of size (area). Instead, he differentiated them along an axis of immigration. Contiguous patches experience the most immigration. A contiguous patch is so well connected to other patches of the same kind that most of the time, when populations inside the patch decline, they are "rescued" by immigration from outside. An island, as Rosenzweig has defined it, is too isolated for this rescue effect to dominate population dynamics. If a given island population declines, it will go extinct unless births on the island – rather than immigration from outside it – turn the tide. But an island is still connected enough to a mainland for immigration, along with extinction, to dominate diversity dynamics. Most of the species on an island owe their presence there to immigration, rather than to speciation on the
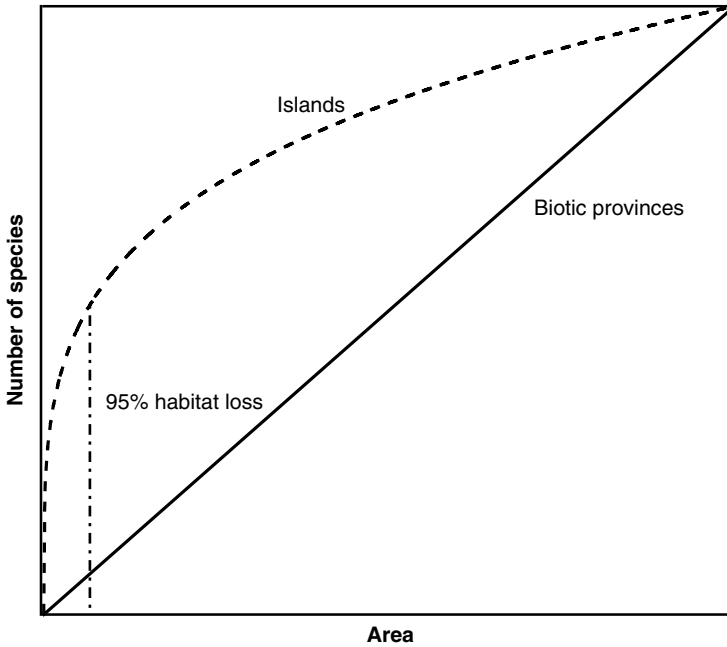
Figure 20.2 Schematic depiction of contrasting relationships between area and number of species

island itself. In contrast, a province is an area so isolated from other, similar habitats that most of its species "arrive" through in situ speciation. For Rosenzweig, Hawaii is isolated enough to count as its own province. But most provinces are much larger.

Rosenzweig's bold claim is that the species-area relationship among provinces is linear, or nearly so. Contiguous patches and islands, in contrast, show a diminishing-returns pattern of species richness with area; Figure 20.2 illustrates the contrast between islands and provinces. If Rosenzweig's claim proves robust, we will have to increase dramatically the estimates of how many species our roadbuilding, agriculture, urbanization, and other avenues of habitat destruction are driving extinct. Importantly, species-area curves provide no information about *how fast* extinctions due to habitat loss will occur. The longer those extinctions take, the more time we will have to restore lost habitat and thereby prevent mass die-offs.

A linear relationship implies that if humans destroy 95 percent of the native habitat in a given province – as we have already done to

the Atlantic rain forest of South America, the tallgrass prairie of North America, and other provinces – eventually 95 percent of the species there will go extinct. In contrast, previous estimates of anthropogenic extinction were based on extrapolation from island curves. Those estimates predicted that losing 95 percent of a province would only drive around 50 percent of its species extinct. To see the contrast, imagine starting with the largest area represented in Figure 20.2 – all the way to the right. Now imagine destroying 95 percent of the habitat – that is, moving 95 percent of the way leftward across the diagram. And note the difference between the fractions of the original species count that the island-based curve versus the provincial line predict to remain.

As the example of plant-herbivore density relations does, the species-area example illustrates how new insights are gained by increasing the scale of ecological investigation. In this case, however, the change in scale resulted in a shift from seeing provinces as open systems analogous to near-shore islands to seeing them as relatively closed. The large proportion of species that are endemic to – that is, found nowhere else than in – particular biotic provinces warrants treating provinces as relatively closed with respect to immigration (though of course not isolated from solar energy input, etc.). This case therefore reminds us that in some cases, and in some respects, there may be good reason to treat a given ecological entity as a closed system.

c. Biodiversity and Ecosystem Function

Besides a trend toward larger scales, another change in the 1990s was a shift from viewing the number of species in a community or ecosystem strictly as a dependent variable – that is, as the *effect* of other ecologically important properties, such as area, as discussed earlier – to investigating its potential role as a *cause* of important ''ecosystem functions'' as well (Naeem 2002). One prominent strand of this research deals with the influence of plant species richness on total plant density. Plant density, in turn, affects the ability of ecosystems to provide ''services'' such as carbon storage, flood and drought control, and wildlife habitat. Darwin asserted a positive effect of species richness on total density, so this is not exactly a new topic (Mikkelson 2004). What is new is the large amount of attention – and
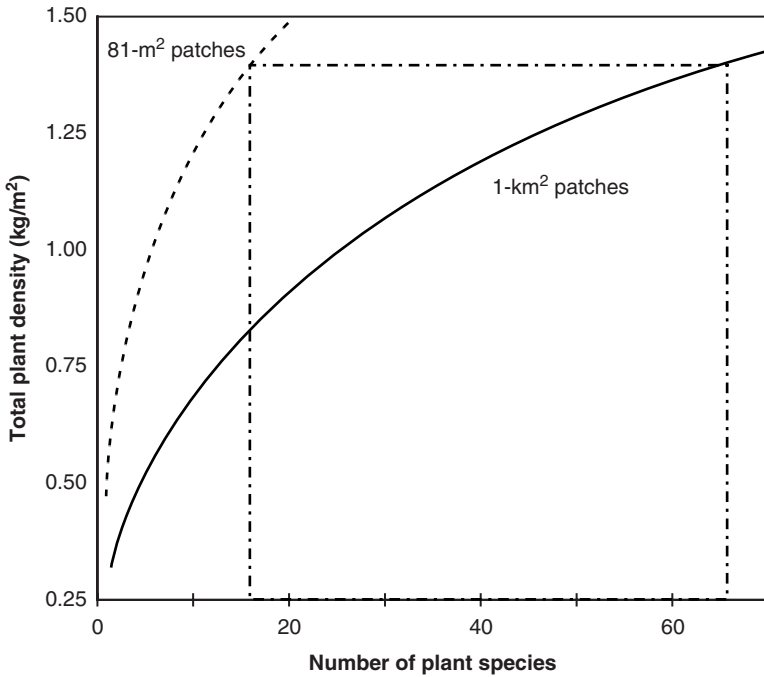
Figure 20.3 Schematic depiction of contrasting relationships between number of plant species and total plant density

controversy – that diversity-density and other diversity-ecosystem-function relationships have recently attracted.

In one experiment, 9-meter by 9-meter (81-m^2) grassland plots sown with more species tended to have substantially greater total density than those planted with fewer species (Tilman et al. 2001). The experimental treatments ranged from 1 to 16 plant species and yielded a range of around 0.4 to 1.3 kilograms/m^2 of total plant density. See the dotted curve in Figure 20.3.[6] For practical reasons, these grassland field experiments and others like it have occurred at scales that are small relative to the size of most farms, let alone larger management units such as national forests or ecoregions.

The species-area law can be used to predict what should happen to the diversity-density relationship at such larger scales (Tilman 1999). At progressively larger scales, it should take more and more species to achieve any given biomass density. For example, we can use a recent estimate of the species-area relation for contiguous

patches to extrapolate Tilman and colleagues' results. According to Rosenzweig (2003), roughly $S = cA^{0.15}$, where S is number of species, c is an adjustable parameter, and A is area. This equation entails that for each 81-m^2 plot in a square kilometer of grassland to contain 16 species, the 1-km^2 patch would have to contain 66 species. Thus, to attain the maximum density realized in Tilman and coworkers' experiment throughout a 1-km^2 patch, it would take 66 species, rather than only 16 (cf. the solid curve in Figure 20.3).

One way to understand this contrast between diversity–total-density relations at different scales is to consider that the larger the patch, the more heterogeneous the temperature, moisture, and soil conditions, and so on, are across it. This means that the particular set of species able to attain a certain total density in one part of the larger habitat will differ from the species that are collectively able to attain the same density in other parts. This, in turn, entails that achieving any given density across a large habitat requires more species than are needed to achieve the same density within any smaller part of it.

3.   MECHANISTIC RESEARCH IN OPEN SYSTEMS

In all three areas of research exemplified in the previous section of this paper, ecologists have sought to go beyond the discovery of so-called phenomenological patterns, by uncovering the "mechanisms" responsible for them. In this section, I aim to correct the misconception that mechanistic research is necessarily reductionistic. This misconception seems common among both philosophers and ecologists, and among both advocates and opponents of reductionism. As one antireductionist philosopher of social science put it, "The microexplanation tells us the mechanism by which the macroexplanation operated" (Garfinkel 1981, 58). Darden criticized another philosopher, Thagard, for his "reductive" view of certain genetic mechanisms (Darden 2000). My argument in the following is similar to Darden's, but more fully developed, and framed within the context of ecology. I have elsewhere spelled out a different, complementary reason why mechanistic research often contradicts, rather than fulfilling, reductionist prescriptions (Mikkelson 2004).

a.   Definitions

Before going further, let us consider what is meant by the words "mechanism" and "reductionism". I submit that in general, to provide a mechanism for an ecological relationship is to "fill in the blank". Given that A causes B, to describe a mechanism for that relationship is to show that A causes M, which then causes B. In other words, the mechanism $A \rightarrow M \rightarrow B$ partly fleshes out the causal pathway $A > B$. This is fairly minimalist compared to the explications discussed by Tabery (2004). I am not convinced that any more is really needed than I provide here, but if more is required, then perhaps my interpretation still works as a partial definition of the term "mechanism", providing necessary, though not sufficient, conditions.

To illustrate this construal of the "mechanism" concept, suppose that an increase in one population causes a second, competing population to decrease. The Lotka-Volterra competition equations – a relatively "phenomenological" approach – can describe this kind of effect with reasonable accuracy. More "mechanistic" models go beyond the Lotka-Volterra equations by specifying *how* populations exert competitive effects on each other. For example, resource-competition equations can represent the following causal chain: An increase in one plant population leads to increased uptake of a certain nutrient by that population, thereby reducing the amount of that resource left in the environment. This decrease in the nutrient supply then causes a second population, dependent on the same nutrient, to decline.

What type(s) of reductionism is (are) at stake in ecology? Schoener seems to have captured at least one important kind. He also assumed without discussion that "mechanistic" means "reductionistic":

[A]dvocacy of a reductionist approach coincides with emphasizing internal, rather than external, factors when simplification is necessary. Thus mechanistic people will stress behavioral and physiological detail at the expense of, say, food-web detail. (Schoener 1986)

Schoener's article focused on explaining population dynamics. His comments therefore imply that mechanistic explanations of such dynamics must involve more detail about the organisms composing the populations than about the communities or ecosystems

containing the populations. In other words, he argued that the mechanisms of population dynamics are predominantly micro- or lower-level.

At the extreme, this form of reductionism entails treating populations as completely closed systems that do not interact at all with macro- or higher levels. The density, for example, of a closed population would be explained strictly in terms of the properties of that population, including the individual organisms within it. Such higher-level phenomena as the densities of other populations, or the total number of species, within the same community, would play no role in reductionistic explanations of this kind.

b.   A Higher-Level Mechanism

Let us now consider the implications of a recent theoretical study that instead treats populations as open systems embedded within ecological communities (Kilpatrick and Ives 2003). The authors of this study offered a mechanistic explanation for "Taylor's law". This law relates the variability of a population to its average density: $\sigma^2 = c\mu^z$. σ^2 is the variance of population density, c is a coefficient greater than zero, μ is mean population density, and z is an exponent less than 2. Ecologists have found this pattern – observed among "more than 400 species in taxa ranging from protists to vertebrates" – interesting because it differs from the "null" expectation. If populations experienced constant per capita variability, z in the equation would equal 2. The fact that z is less than 2 for most species means that an increase in population density leads to a decrease in per-capita variability.

Kilpatrick and Ives explained this pattern in terms of populations' "diffuse interactions" with the other species in their communities. Roughly speaking, their mechanism works as follows: Any given "focal" population undergoes some variation due directly to fluctuations in its physical environment. Fluctuations in the populations of its competitors add a second source of variation in the focal population. Suppose that the focal population experiences a permanent increase in its mean density. Other factors being equal, this would force a decrease in the mean densities of at least some of its competitors.[7] This, in turn, would reduce the pressure exerted by those competitors on the focal population. Each member of the focal

population would then be less affected by fluctuations in the densities of these competitors. If the direct contribution of environmental ''noise'' to per-capita variability remains the same, then overall per-capita variation in the focal population should decline.

We thus have an example of a higher-level mechanism for a same-level relationship. This is a different sense of ''higher-level mechanism'' than the one Glennan attributes to Wimsatt (Glennan 2002). The latter refers to any mechanism that does not ''plunge'' all the way down to some ''fundamental'', such as microphysical, level. In contrast, here I mean a mechanism that involves properties at a higher level than the relationship being explained. In this case, a community-level mechanism explains a population-level relationship, Taylor's law. This case therefore contradicts the common assumption, implied by Garfinkel (1981) and expressed by Schoener (1986), that mechanisms entail reductionism. In other words, this case demonstrates that mechanistic research need not emphasize the parts of a focal entity at the expense of its context or environment.

Incidentally, the two examples cited in this section also illustrate the relativity of the phenomenological/mechanistic distinction. The Lotka-Volterra competition equations are phenomenological relative to resource-competition equations. But relative to Taylor's law, the Lotka-Volterra model that Kilpatrick and Ives used to describe *how* mean population density affects population variability is mechanistic.

CONCLUDING SUMMARY

In this essay, I have described a recent shift in perspective from smaller to larger scales in ecology. This shift has revealed that species diversity is more important, and under greater threat, than was previously known. It also motivates greater appreciation of the role played by higher-level causes in nature. I have also illustrated how recognizing the open character of most ecological systems leads naturally to the discovery of higher-level mechanisms. Earlier in the chapter, I situated these points within the context of recent work in the philosophy of ecology. And I framed the discussion in terms of logical positivism's tenacious legacy.

NOTES

1. Living mass per unit area or volume.
2. Many of these surveys actually involved algae, which, strictly speaking, are not plants but play the same ecological role as plants, namely, ''photosynthesizer'' or ''primary producer''.
3. Those familiar with food chains know that this scenario presupposes an even number of trophic levels (e.g., just plants and herbivores, or plants plus herbivores plus ''primary'' carnivores plus ''secondary'' carnivores'').
4. Represented in Leibold's paper by ''Model 1''.
5. Leibold's Models 2 and 3.
6. Estimated by visual inspection of the Year 2000 data shown in figure 1B of Tilman et al. (2000).
7. Even if the increase in the focal population did not reduce other populations, it would still reduce their *relative* densities – relative, that is, to the density of the focal population.