

CHAPTER 3

A General, Unifying Theory of Ecology?

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Samuel Scheiner and Michael Willig (Chapter 1) have provided a philosophical framework for understanding ecological principles, theories, and models. Fundamentally, they contend that contrary to many ecologists' views about their own discipline, ecology already possesses a general, unified theory. In this essay, I first present their framework. Second, by way of comparison, I consider the work of the population and community ecologist Robert MacArthur. MacArthur's own work was thought of as providing unifying theories. In contrast, I argue it focused more specifically on integrative theories and models. Finally, I expand on several points in the Scheiner and Willig framework.

The Scheiner-Willig framework

According to Scheiner and Willig (SW), a theory in the sciences consists of two elements, a set of principles and a domain (Chapter 1). What is the domain of ecology? According to SW, it is the spatial and temporal patterns of the distribution and abundance of organisms, and includes the causes and consequences of those ecological processes (Chapter 1). Lest one think this is too "organism-focused," it includes biotic and abiotic factors that affect organisms along with groups of organisms at a variety of levels including populations, communities, and ecosystems. The principles describing this domain are selected on the basis of two criteria (Scheiner and Willig 2008): an inclusionary

rule (for something to be a principle of a given domain, the principle must be shared by many constituent theories of that domain) and an exclusionary rule (for something to be a principle of a given domain, it must distinguish this domain from some other distinct domain).

Put simply then, something is a principle of a given domain if, and only if, it is shared by the constituent theories of that domain and is not shared with constituent theories of a distinct domain.

So what are the basic principles of this general and unified theory of ecology? They are principles that ecologists already accept given the domains they study. In a way, SW are simply making those principles explicit. More importantly, they are presenting them together, which highlights their role in structuring ecological thought collectively. Although ecology may appear to be a fairly disunified discipline, there is actually much unity undergirding various theories and models. See Table 1.3 for their list of these unifying principles.

SW recognize that theories come in degrees of generality or abstractness. They distinguish between general theory, constituent theory, and models (Chapter 1). A general theory consists of confirmed generalizations that are abstracted from facts that have been systematically tested. Using general theory in addition to more concrete considerations, we can arrive at constituent theories. A constituent theory consists of confirmed generalizations or laws, and from them models may be derived. Finally, there are models that are propositions by which hypotheses can be articulated and evaluated. Thus, there is a hierarchy of theoretical structures that become less abstract as one moves down the hierarchy. The principles of the general theory are listed above and the constituent theories include succession theory, foraging theory, metapopulation theory, and many others.

As a particular example of the SW framework, consider work on predator-prey theory. There are several general principles that can be used to derive constituent theory concerning predator-prey relationships that include the claim that organisms interact with their abiotic and biotic environments, resources are finite and heterogeneous in space and time, and birth rates and death rates are a consequence of interactions with the abiotic and biotic environment. Let's assume that the growth rate of the prey is determined by the growth rate of the prey population independent of the predator minus the capture rate of prey per predator multiplied by the number of predators, and that the growth rate of the predator population is determined by the rate at which each predator converts captured prey into predator births minus the rate at which predators die in the absence of prey multiplied by the number of predators. Here we have a classical theory of predator-prey interactions. From this we can derive more concrete models that may be tested by data. For example, let's

further assume as Lotka-Volterra models do that the prey grows exponentially in the absence of the prey, predator and prey encounter one another randomly in proportion to their abundance, the predators have a linear functional response, the numerical response of the predator is a constant multiplied by the functional response, and the predator declines exponentially in the absence of the prey. Here we start with general principles, add detail that results in a constituent theory, and then arrive at a model only once we have added, in this case, quantitative detail. It is crucial to note that from general principles one can derive many different constituent theories and from them many different models. We could have devised a different model by assuming a different type of functional response for example.

Each of the principles above can be found in different areas of ecology, though articulated in different ways. For example, consider principle one—organisms are distributed in space and time in a heterogeneous manner. In population ecology, organisms are distributed unevenly as a population over a habitat. For example, they may be distributed unevenly vertically in a lake or in a forest (Begon et al. 1996b). Likewise, in metapopulation theory, organisms are grouped into a population of populations, and their dynamics are largely controlled by local extinction and migration amongst distinct patches. This may be the case with forest patches or oceanic islands (Hanski and Gilpin 1997). Similarly, in landscape ecology, we see organisms distributed in different ecosystems or biomes (Turner et al. 2001). Depending on the subdiscipline of interest, each of these principles can be made concrete in different ways. As another example, consider the third general principle—variation in the characteristics of organisms results in heterogeneity of ecological patterns and processes. In behavioral ecology, the characteristics of interest involve different foraging strategies such as being generalist or specialist; in life history theory it may involve the characteristics of being an annual or perennial plant. Finally, consider the principle that the distributions of organisms and their interactions depend on contingencies. We can see how this principle is made concrete in different ways by considering the introduction of stochastic growth rates in population ecology and in community ecology through the notion of “ecological drift” in neutral theories of biodiversity.

The fact that ecological theory is composed of this hierarchy of general principles, constituent theories, and models has fundamentally important implications for evaluating general principles, constituent theories, and models. Specifically, it challenges an excessively narrow Popperian view of theory testing in ecology (Peters 1991). Suppose a model fails some particular test or tests. This does not necessarily impugn the constituent model from which it was derived nor the general principles on which it is based. The general princi-

ples and constituent theories are made concrete in models based on the particular domains, assumptions, backgrounds, and definitions that are considered. Thus, one falsifies a general principle only after many different constituent theories and models have been evaluated in light of the relevant facts.

SW have focused on the notion of generality and unification as the relations that exist between ecological theories and data, about which more will be said below. However, I now will introduce what I believe is a different conception of how theories relate, namely that of integration. As an example, consider the work offered by the eminent ecologist Robert MacArthur.

MacArthur's integrative approach

Robert MacArthur stands as one of the most influential and controversial ecologists ever to work in the discipline (Fretwell 1975; Pianka and Horn 2005). He is recognized for having done exceptionally original theoretical and empirical work. However, many believe that he took ecology down the wrong path both theoretically and methodologically. As an example, MacArthur and his colleagues' work on limiting similarity is often seen in this light (MacArthur and Wilson 1967; May and MacArthur 1972). The project was to understand why species are spaced along resource spectra given their niche breadths and widths respectively. The MacArthurites argued that there is some maximum degree of similarity in resource use such that a set of species can coexist. However, it was argued that this theoretical claim was argued to be very fragile given the assumptions made in the models and did not hold up with respect to the data (Abrams 1983). Independent of one's opinion on this matter, MacArthur's work serves as an interesting case study. He too attempted to provide a framework for understanding how ecological theories relate to each other. However, in my mind, it was not a unificationist but an integrationist approach. More on this later; first, a bit of history (for more details, see Odenbaugh 2006).

In July 1964, Robert MacArthur, Edward O. Wilson, Egbert Leigh, Richard Levins, Leigh van Valen, and Richard Lewontin met at MacArthur's lakeside home in Marlboro, Vermont. The subject of their conversation was their own research in evolutionary genetics, ecology, and biogeography, and the overall future of what is termed "population biology." Ironically, the subject matter of these conversations was not simply population biology understood as population genetics, population ecology, and possibly ethology. It clearly included disciplines like community ecology, macroevolution, and biogeography, given the sorts of models formulated and questions asked. More importantly, there was a general tendency to approach these areas with mathematical theory as represented in theoretical population biology. For two days, each

participant discussed their work and how a "central theory" could be achieved (Wilson 1993, pp. 252–253). The work that resulted from these collaborations was important and changed much of evolutionary and ecological theory. In 1972, collaborator E. O. Wilson and mentor G. E. Hutchinson wrote the following of MacArthur after his death.

[He] will be remembered as one of the founders of evolutionary ecology. It is his distinction to have brought population and community ecology within the reach of genetics. By reformulating many of the parameters of ecology, biogeography, and genetics into a common framework of fundamental theory, MacArthur—more than any other person who worked during the decisive decade of the 1960s—set the stage for the unification of population biology. (Wilson and Hutchinson 1982, p. 319)

Did MacArthur and his coworkers "unify" evolution, ecology, and biogeography? I will argue contrary to Wilson and Hutchinson that he did not do so.

To assess MacArthur's accomplishment, we must understand the components of the program he and others articulated. Here are some of the elements. First, MacArthur typically formulated general, simple deterministic models that lacked precision. In the terms of Richard Levins' account of model building, precision was sacrificed for generality and realism. This is not to say that MacArthur modeled ecological systems realistically; rather, the desiderata of interest were generality and realism, and precision less so. As an example of MacArthur's "realism," he devised a mechanistic consumer-resource model with two consumers and two resources, and showed how the more phenomenological Lotka-Volterra interspecific competition model could be derived from it (MacArthur 1972). Second, MacArthur also emphasized the ecological process of interspecific competition as a mechanism structuring ecological communities. This is evident in his work on limiting similarity and species distributions (i.e., the broken stick model). This is not to say that he did not work on other types of processes like predation (MacArthur 1955); rather, interspecific competition played a predominant role in his thinking. Third, MacArthur rarely evaluated model predictions statistically. There are of course exceptions to this rule, but mostly he and his colleagues evaluated models by looking for corresponding dynamical patterns such as stable equilibria and various types of cycles. Finally, he was a master at presenting complex mathematical results with graphical representations (MacArthur and Levins 1967; MacArthur 1970a). Specifically, MacArthur used isocline analysis to not only present theory in pedagogically useful ways but also to draw interesting and

unobvious implications (Rosenzweig and MacArthur 1963), a hallmark of good theory.

MacArthur and his colleagues produced a variety of different models involving environmental heterogeneity, density-dependent selection, optimal foraging, limiting similarity, and equilibrium island biogeography. As an example of MacArthur's theoretical work, let us consider his modeling of density-dependent selection. This is a case where MacArthur attempts to integrate ecological and evolutionary concepts that connects to several of SW's principles (specifically principles two, five, and eight).

In most evolutionary models according to MacArthur, population geneticists use r , the intrinsic rate of increase of a population, as a measure of fitness. He writes, "For populations expanding with constant birth and death rates, r , or some equivalent measure (Fisher used r ; Haldane and Wright used e^r which Wright called W) is then an appropriate definition of fitness" (MacArthur 1962).

However, as MacArthur notes, present values of r may not be reliable predictors of the number of descendants a group of individuals will have because r is an accurate measure of fitness only if the environment is relatively stable. One way in which the environment may be unstable is if population density affects fitness. In fact, MacArthur writes, "to the ecologist, the most natural way to define fitness in a crowded population is by the carrying capacity of the environment, K ." (MacArthur 1962, p. 146). MacArthur offers the following mathematical model. Let n_1 and n_2 represent populations of alleles 1 and 2, respectively, and let them be governed by the following equations:

$$dn_1/dt = f(n_1, n_2) \quad (3.1)$$

$$dn_2/dt = g(n_1, n_2) \quad (3.2)$$

To understand this model, it is simplest to examine it graphically (Fig. 3.1).

Suppose we have a phase space where the x -axis represents the population of allele 1 n_1 and the other y -axis represents the population of allele 2 n_2 . Thus, a point in the space represents the joint abundances of population n_1 and n_2 . Suppose there is a set of values of n_1 and n_2 such that there is a solution $f(n_1, n_2) = 0$, or equivalently, $dn_1/dt = 0$ for those values of n_1 and n_2 . If the population of n_1 is to the left of the f -isocline, then it will increase. Likewise, if the population of n_1 is to the right of the f -isocline, then it will decrease. Let us further suppose that there are a set of values of n_1 and n_2 such that there is a solution $g(n_1, n_2) = 0$, or equivalently, $dn_2/dt = 0$ for those values of n_1 and n_2 . If the population of n_2 is below the g -isocline, then it will increase. Likewise, if the n_2 population is above the g -isocline, then it will decrease.

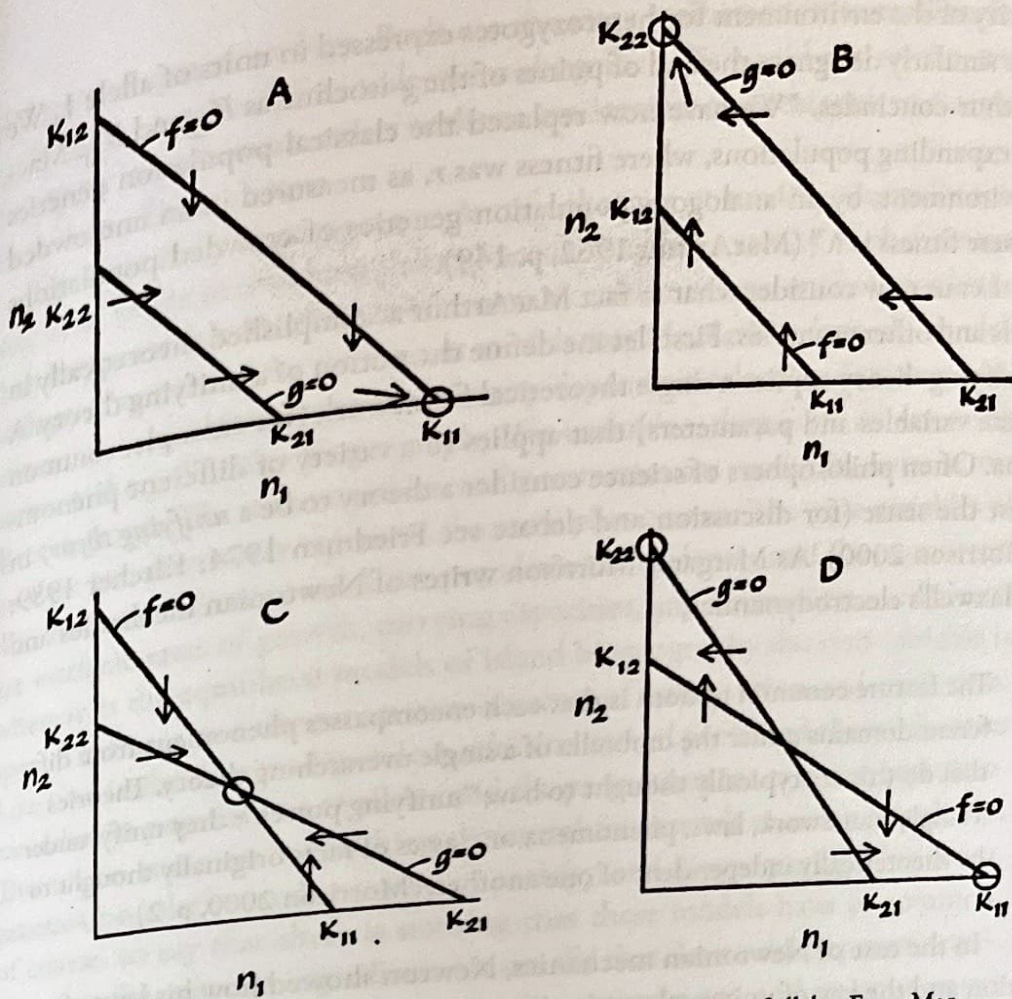


Figure 3.1 Density-dependent selection and competitive exclusion of alleles. From MacArthur and Wilson 1967, p. 147.

There are four different ways the two isoclines can relate to one another. In part A of Fig. 3.1, we can see from the vector arrows that allele 1 will outcompete allele 2. Likewise, in part B, allele 2 will outcompete allele 1. In part C, the vector arrows show that there is a stable equilibrium between allele 1 and 2. Finally, in part D, whichever allele is more frequent at the outset will outcompete the other.

We can now explain how this model represents both ecological and evolutionary features. The $f=0$ isocline intersects the axis at the value K_{11} . In this circumstance, the population consists only of allele 1, and K_{11} represents the number of allele 1 homozygotes that can maintain themselves in this environment. In other words, K_{11} is the carrying capacity of the allele 1 homozygotes. Likewise, the $f=0$ isocline intersects the axis at the value K_{12} . K_{12} is the number of allele 2 that can keep allele 1 from increasing and represents the carrying ca-

lating many of the parameters of ecology, biogeography, and genetics into a common framework of fundamental theory." We can now see how MacArthur approached the relations between theories. Here is another definition. An *integrating theory* takes a variety of theories (different state variables and parameters) and combines them in their application to a variety of phenomena. He supplied a variety of models that incorporated many different evolutionary and ecological state variables and parameters, thus taking a first step toward integrating population biology.

The SW program differs from the MacArthur program in that it explicitly looks for *common* principles across ecology's subdisciplines, whereas the MacArthur program was looking for "piecemeal" connections. In fact, we can "harmonize" the SW and MacArthur programs if we recognize that both are emphasizing different parts of the theoretical hierarchy. SW have worked hard in identifying the key general principles that constituent theories and models share. MacArthur spent most his time attempting to articulate novel constituent theories and more specifically models for understanding the distribution and abundance of organisms. Thus, unification and integration are regions along a continuum. Unification is largely to be found at the most abstract level of the theoretical spectrum. Integration, on the other hand, is to be found at the level of constituent theories and models. These two features of theoretical structures are points of emphasis and are complimentary.

Having said this, MacArthur at times was clearly engaged in the same project as SW. MacArthur most famously wrote,

Science should be general in its principles. A well-known ecologist remarked that any pattern visible in my birds but not in his *Paramecium* would not be interesting, because, I presume, he felt it would not be general. The theme running through this book is that the structure of the environment, the morphology of the species, the economics of species behavior, and the dynamics of population changes are the four essential ingredients of all interesting biogeographic patterns. Any good generalization will be likely to build in all these ingredients, and a bird pattern would only be expected to look like that of *Paramecium* if birds and *Paramecium* had the same morphology, economics, and dynamics, and found themselves in environments of the same structure. (MacArthur 1972, p. 1)

Clearly, MacArthur believed that there were general principles concerning morphology, economics, and dynamics that would be made concrete in possibly different ways in different constituent theories and models, depending on the taxonomic group under study.

Elaborating on the SW program

Let us now turn again to the SW program. First, how do we distinguish between general theory, constituent theory, and models? Are they different in kind or degree? One thing one might argue is that they are not different in kind but vary continuously along some dimension. For example, a principle is more general than another when the former's domain is a superset of the former's domain; or conversely a domain is a proper subset of another. However, one might also argue that structures differ in kind. For example, it is customary to believe theories comprise a small set of natural laws. Consider Newtonian mechanics with its three laws of motion and gravitation as familiar case in point. Models, on the other hand, are often thought of as not consisting in natural laws at all; rather, they are idealized representations of natural systems without natural laws. If this is so, then theories and models are distinct. So, there is a general question about how these different sorts of structures relate to one another.

Second, biologists make much out of the notion of *contingency*, and SW do so in principle three. However, what is "contingency"? In what sense it is a cause of the ecological patterns? There is much work to be done clarifying the role of contingency in ecological theories. Here is one way of construing contingency. An effect variable Y is *contingent* on a causal variable X to the degree that slight changes in values of X greatly change values of Y . Of course, this is just sensitivity to initial conditions—a species of nonlinearity—and there are various quantitative measures of it. Moreover, we could generalize with regard to a multivariable system where small changes in a set of causal variables $X_1, X_2, X_3, \dots, X_n$ lead to a large change in the effect variable Y . In the way that I have characterized contingency, it is not a cause of anything; rather, it is a pattern concerning causes and their effects.

Third, SW claim that evolution causes the ecological properties of species. As the eminent ecologist G. E. Hutchinson (1965) argued, ecology is the theater of the evolutionary play. Put less metaphorically and only in terms of natural selection, ecological processes create selective regimes. These ecological processes cause or determine mechanistic or proximate differences in reproductive success. One way of construing SW's insight is that they are insisting that *current* ecological processes are in play because of *past* evolutionary processes. Hutchinson's idea can then be coupled to this proposition with the claim that *current* evolutionary processes are in play because of *past* ecological processes. Thus, properly understood, ecological and evolutionary processes are spatiotemporally interdependent. Thus, there is a crucial interaction between ecological and evolutionary processes.

Finally, where does ecosystem ecology fit in the prescribed domain of the

abundance and distribution of organisms? The domain of ecosystem ecology is roughly the cycling of nutrients and flow of energy. For example, ecosystem ecologists focus on the nitrogen and carbon cycles or gross and net primary production. One could and some do argue that ecosystem ecology really just is biogeochemistry and not ecology per se since organisms—the currency of ecology and other biological sciences—have disappeared from the science (Cooper 2003). However, in my view, this would inject a bias in favor of population and community ecology and the history of ecology has been ensconced with ecosystem ecology just as much as these other disciplines. In fact, historians of ecology have spent more time writing about ecosystem ecology than about population or community ecology. I am unsure of why this is, but it is an interesting fact about the history, or historians, of science.

If ecosystem ecology is a genuine branch of ecology as I have suggested that it is, then this is where an integrative framework is important since it can couple energy flows and nutrient cycles with food web dynamics for example. Of course, there may be even more general principles one can provide that bring ecosystem, community, and population ecology together.

Conclusion

In this essay, I have presented the SW unification framework and have also presented a similar though importantly different integrative framework through the work of Robert MacArthur. Importantly, unification concerns finding the most general principles of a domain, and integration consists in bringing together different constituent theories and models. However, unification and integration are complementary because they concern different regions of the theoretical hierarchy. I also considered some specific elements of the SW framework including the notion of contingency, the relationship between ecology and evolution, and the place of ecosystem ecology in their general principles. Whether SW have provided a complete account of the unifying principles of ecology or not, they have certainly made an excellent and productive start.

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Constituent Theories of Ecology