

THE SCHISM BETWEEN THEORY AND ARDENT EMPIRICISM:  
A REPLY TO SHIPLEY AND PETERS

In replying to Shipley and Peters (1991), I will focus more on their philosophical points than on a repetition of points already discussed (Shipley and Peters 1990; Tilman 1991). Shipley and Peters are members of a school of thought that has fostered a highly empirical approach to ecology. The detailed analyses of empirical data by members of this group have provided solid descriptions of many ecological patterns and thus contributed greatly to the discipline. I am concerned, however, that their papers (Shipley and Peters 1990, 1991) suggest the existence of a schism between theoreticians and empiricists. They accept as "true" the results of their own experiments, which, when analyzed by regression, explained only 4% of the variance in their data, which were only significant at the  $P \leq .05$  level in one of two comparisons, which had questionable methods that may have biased their results (Poorter and Lambers 1991), and which contradict many published studies (e.g., review in Poorter 1989; Poorter and Remkes 1990). They asserted that this weak evidence totally disproved a theory, even though the suite of species they studied fell outside the stated bounds of that theory. Their willingness to accept weak empirical data but their demand that a theory be universally true suggests a lack of understanding of the role of theory. In proposing my theory, I said that the simplified version (used by Shipley and Peters) applied to plants that had much greater differences in morphology than in physiology. The species chosen for study by Shipley and Peters were similar morphologically but likely had quite different physiologies (see Tilman 1990a). It is not at all surprising that their results did not fit the simplified version of the model.

Ecological research, like all science, is most effective if it is based on the continual interplay of observation, hypothesis generation (theory), and experimentation. Empiricism is clearly a part of this process, as is theory. However, Shipley and Peters suggest that the falsification of one prediction of a mechanistic model indicates that the model is "wrong" and thus not useful in explaining other patterns. This is an extreme, absolute interpretation that sees a model as the mathematical embodiment of ecological truth. In contrast, mathematical ecologists view models as abstractions (e.g., Schaffer 1981)—simplifications that, in the words of May (1973, p. 12), are "caricatures of reality, and thus have both the truth and falsity of caricatures." All models are caricatures, even the models of chemistry and physics, which can be precise predictors for some phenomena but wrong for others.

I often call my models "mechanistic." Shipley and Peters interpreted this to mean that they must incorporate the irrefutable underlying mechanisms that cause

a process. In contrast, I call my models "mechanistic" to distinguish them from classical models that are more phenomenological. This distinction was elaborated in Tilman (1989, p. 94): "Clearly, phenomenology and mechanism are not absolute entities but idealized ends of a spectrum. Any theory that explicitly includes environmental constraints and organismal trade-offs will be more mechanistic than most current theory. It is likely that, along the spectrum from phenomenological to mechanistic theory, there will be a point that is optimal for explaining any given ecological pattern. It is very possible to produce theory that is too mechanistic, that loses generality without gaining significant predictive power. The optimal point will be found only through the usual trial-and-error process of science. It is always possible to produce a theory that is more or less mechanistic than a given theory. I do not propose mechanistic theory as an absolute good, but rather suggest that many present theories may lack predictive power because they are not sufficiently mechanistic, that is, they do not explicitly deal with environmental constraints and organismal trade-offs."

Shiple and Peters asserted that mechanistic models necessarily become increasingly complex, that scientists become seduced by this complexity and delude themselves into believing that they have explained nature. Regression analysis, presumably, allows scientists to avoid this fate. In contrast, I have argued repeatedly that one of the major strengths of mechanistic models is that they are often simpler than traditional phenomenological models (Tilman 1982, 1989). May (1977) suggests that the usual progression of science is from detailed models that include numerous ecological processes to much simpler models that embody their most essential features. Schaffer (1981) and Takens (1981) have developed a mathematical basis for such simplification by demonstrating how a simple model, if properly constructed, can abstract the essence of a much more complex system of equations. Schaffer (1981), Schaffer and Kot (1985), and others have discussed the ecological applications of such abstraction. It is a property of all abstractions that they highlight some traits of a system, sketch others, and ignore still others. Despite this, simple models that use appropriately abstracted variables can be good predictors of ecological patterns because their parameters include information abstracted from the more detailed underlying mechanisms that are not explicitly included in the model. The challenge that we face is in finding the best level of abstraction, namely, the best point on the spectrum from phenomenology to mechanism. Absolute mechanistic causes are not the domain of ecology or any science.

A major purpose of formulating a model as rich in mechanistic detail as Allocate was to determine the extent to which it could be approximated by simpler models. Recent experimental and theoretical work (Tilman 1990a, 1990b; Wedin 1990; Tilman and Wedin 1991a, 1991b) suggests that the  $R^*$  concept ( $R^*$  is the concentration of the limiting soil nutrient in an equilibrium monoculture of a species; Tilman 1982) is such an abstraction. The species with the lowest  $R^*$  for soil nutrient is predicted to competitively displace all other species from habitats in which that is the only limiting resource (Tilman 1982). This single variable abstracts the effects of the morphological and physiological traits of a plant on its

nutrient competitive ability (Tilman 1990*b*). Thus, a single, measurable number can replace numerous physiological and morphological traits. However, these underlying plant traits and  $R^*$  represent different levels of mechanistic detail, and each is useful in its own right. The physiological and morphological traits are a closer approximation to underlying causes and provide a context that explains interspecific differences in  $R^*$  and, thus, in nutrient competitive ability (Tilman 1990*b*; Tilman and Wedin 1991*a*). The simpler, abstracted variable,  $R^*$ , can be measured on numerous species and used to predict patterns in natural, multi-species communities (Tilman 1990*a*; Wedin 1990; Tilman and Wedin 1991*b*).

Thus, there is a level of mechanistic detail that best fits the type of question being asked. The search for mechanism and predictive ability is a search for the appropriate level of abstraction. This search is seductive not because one gets lost in a morass of mechanistic detail (as Shipley and Peters suggested) but because it ultimately allows a better understanding of the simple forces that have shaped nature.

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