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Beyond reductionism and scholasticism in plant community ecology

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Abstract

Recent progress in plant population biology is often used to argue that most questions in community ecology should be answered using a reductionistic approach. This progress may, however, be attributed to at least two other factors: (1) greater emphasis on clear questions with testable alternatives, and (2) greater agreement upon the important variables which describe the systems of interest. In plant community ecology there has been a tendency to collect data rather than pose clear questions, and there is lack of agreement on which community properties are most useful to measure. As a consequence, there is sometimes a tendency to debate concepts instead of posing clear questions. Other more productive avenues for community level ecology exist.

Introduction

Since the publication of Harper's (1967) paper entitled 'A Darwinian approach to plant ecology', there has been rapid growth in plant population biology (e.g., Harper, 1977; Stearns, 1977; Solbrig *et al.*, 1979; Dirzo & Sarukhan, 1984). This growth is frequently contrasted with that in plant community ecology and/or vegetation science, followed by the conclusion that reductionism is therefore the avenue to advancement in community ecology.

My own interpretation of Harper's paper is that the reductionism–holism interpretation overlooks two other equally important messages. Both of these messages apply equally well to any level of organization being investigated. Here I will discuss them in the context of the community level of organization. Studies at this level of organization are variously called 'plant community ecology' or 'vegetation science', with vegetation science often associated more strictly with phytosociology. Since these comments are directed simply at the community level of organization, I will not emphasize such distinctions.

Let us reconsider two aspects of Harper's paper in turn. He first reiterates the conceptual framework of population biology (evolution) and using it poses a series of questions. The same conceptual framework is then used to propose dependent variables which must be measured to answer these questions.

Questions

There is frequently less emphasis on precise questions at the community level of organization. This lack of emphasis on questions, or testable hypotheses, may result from what might initially seem to be a strength of such research: the relative ease with which data can be collected. It is so easy to collect descriptive data in plant community ecology, however, that there is always the temptation to start sampling quadrats just to see what happens or in

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hope that the data will be useful someday. There is also, as a consequence, a strong emphasis on statistical methods for manipulating large data sets. Neither vegetation description, nor new statistical techniques, can themselves produce scientific advancement. They should be treated as just two of many possible tools available for answering questions. Perhaps community ecology would develop more rapidly if we all hung up our quadrats for a few years and instead tried to decide what questions we need to answer.

This is not to completely deny the value of purely descriptive studies. Phytosociology has at least two useful roles. The first is to provide a vegetation classification for resource management, including the systematic selection and management of nature reserves. The second is to generate hypotheses regarding vegetation processes which can then be experimentally tested. While there are many examples of the former, there are relatively few of the latter. Goldsmith's studies on sea cliff vegetation (1973a, b, 1978) illistrate the way in which descriptive multivariate studies can be used to generate questions, and the role of experiments in answering such questions. Many purely descriptive studies, however, do not pose meaningful questions about ecological processes, much less propose how such questions could be answered experimentally.

Measurable dependent variables

The second strength of Harper's paper is the emphasis upon measurable dependent variables. Evolution provides strong clues as to what variables are important to measure: they are traits which determine an organisms's contribution to future generations. In the absence of a similar conceptual framework at the community level of organization, there has been a tendency to concentrate on descriptions of species composition as if only taxonomic names could describe communities. In contrast, when more holistic variables such as diversity and biomass are considered, patterns at the community level emerge clearly (e.g., Al-Mufti *et al.*, 1977; Grime, 1973, 1979; Silvertown, 1980; Tilman, 1982, pp. 123–132, Wheeler & Giller, 1982; Del Moral, 1983, 1985; Menges & Waller, 1983; Wilson & Keddy, 1986). The resulting relationships are not only consistent across many vegetation types, but also allow predictions of vegetation responses to changes in factors such as grazing or fertilization.

Variables such as biomass and diversity are not the only ones which can describe vegetation; Grime (1979) proposes that traits such as physiology, life form, phenology, demography and morphology vary predictably within plant communities. Systematically screening large numbers of species for specific traits then provides new variables for describing communities; two recent examples are maximum relative growth rate (Grime & Hunt, 1975) and germination patterns (Grime, 1979; Grime *et al.*, 1981). These methods of 'comparative plant ecology' have the potential to produce important new dependent variables for describing plant communities.

Concepts and theories

The interaction between clearly defined questions and measurable traits of vegetation cannot be overemphasized. Clearly defined questions generate alternative hypotheses which are testable, and measurable variables provide the means to test the hypotheses. If either of these is missing, the process of discovery is hindered, if not entirely halted. Thus, some of the questions asked in vegetation science (e.g. continuum vs. community unit concept) have not been productive because they relate to concepts rather than hypotheses (sensu Peters, 1980). That is, they are stated in a non-testable form rather than as explicitly defined relationships among measurable quantities. In examining the decades of publications on concepts such as the continuum vs. community unit organization of vegetation, it seems reasonable to conclude that 'we have become modern scholastics interminably discussing questions which cannot be solved or tested scientifically' (Peters, 1980; Stearns, 1976). In re-examining the continuum as opposed to the community unit concept, for example, Shipley & Keddy (1987) have argued that existing concepts

generate four mutually exclusive hypotheses rather than two. Moreover, when inferential statistics are used to try and test these hypotheses, both the 'continuum' pattern and 'community' pattern are falsified and a third alternative accepted.

In conclusion, I have suggested that the two most important points in Harper's paper have little to do with reductionism, but rather with the application of certain scientific methods. These scientific methods are not in any way new, but are reiterated here for two reasons. First, there is no reason to assume that plant population ecology is the only, or even the best route to explore plant communities – indeed, it has conceptual and methodological problems of its own (Stearns, 1976, 1977). Second, community ecologists have, on occasion, consumed large amounts of time and energy discussing poorly defined concepts rather than posing clear questions and specifying the variables which must be measured to answer these questions.

The search for theories and models in vegetation science (the theme of this symposium) seems most likely to succeed if clear questions about community level phenomena are posed using measurable variables. What is less clear is which questions, and which variables, will produce the rapid progress, rigorous predictions and broad generalizations we require.

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