

Forum

It's About Time: A Critique of Macroecological Inferences Concerning Plant Competition

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Several macroecological studies have used static spatial data to evaluate plant competition in natural ecosystems and to investigate its role in plant community dynamics and species assembly. The assumptions on which the inferences are based have not been consistent with ecological knowledge. Inferences about processes, such as competition, from static data are weak. Macroecology will benefit more from dynamic data, even if limited, than from increasingly sophisticated analyses of static spatial patterns.

Macroecology (i.e., the study of ecosystems using a ‘top-down’ approach at large spatial scales to characterize patterns of abundance, distribution, and diversity [1]) has been successful in detecting broad ecological patterns. The value of using large ecological data sets that cover substantial parts of the world and include wide climatic gradients to develop and test general ecological hypotheses is widely recognized. Here, we emphasize a critical limitation of most studies, one that needs to be overcome if macroecology is to fulfill its potential. We focus on one process as an example of this general problem: competition among plant species.

Competition Among Species

Competition among neighboring plants arises because the resources needed

for plant growth and reproduction are limited and contested, and a plant that extracts or monopolizes more of a limiting resource will grow faster and reproduce in greater numbers than another that obtains less. In principle, it should be possible to examine competition for limiting resources if there is sufficient knowledge of the resource levels and the physiological processes of the competing plants. However, in most terrestrial ecological studies, there is little, if any, information on the uptake and dynamics of the resources that limit the growth of different plant species. Instead, competition is inferred from observed negative effects of neighboring plants on growth without information about the resources for which the plants were competing. Competitive interactions generally have been measured either: (i) by measuring biomass at a known initial plant density in manipulated and replicated competition experiments [2,3]; or (ii) by measuring the effect of the neighboring plants on the growth of the target species in a time-series study [4,5].

The important common feature of these two general methods of measuring competition is that they are based on dynamic data. A single measurement in time does not tell us anything about processes. One needs to know the initial density or rely on a time series to measure the effect of neighboring plants on plant growth (i.e., information on the change in plant biomass from one time period to the next). Just as one needs more than one measurement in time to measure a velocity or a rate, one needs more than one measurement in time to measure the effect of the neighboring plants on the growth of target plant species.

Unfortunately, good ecological time-series data (i.e., longitudinal plant abundance data), which are needed to fit empirical plant population ecological models and make strong inferences concerning the mechanisms of plant–plant interactions are sparse. In the endeavor to test broad ecological hypotheses addressing the

mechanisms of plant–plant interactions and their role in plant community dynamics and species assembly processes on a large spatial scale, it is tempting to circumvent this lack of ecological time-series or experimental data and construct *ad hoc* methods where assumptions, which are often questionable, are used on available large-scale plant abundance data. Here, we discuss two representative examples.

Unjustified Assumptions

One type of assumption that often is used to infer plant competitive mechanisms from static spatial data sets is that the biomass of neighboring plants is used as a proxy for interspecific interactions. For example, a recent article [6] states ‘...we also collected the above-ground biomass of all other herbaceous species in each subplot as a proxy for interspecific interactions. Despite being an indirect measure, biomass production by neighbouring individuals is widely used to reveal the outcome of interspecific interactions (Tillman & Wedin 1991; Campbell & Grime 1992), ...’. This assumption is widely used, but it is usually unfounded; neither is it corroborated by the two studies cited, which describe carefully designed and replicated competition experiments. One problem with using the biomass of neighboring plants as a proxy for interspecific interactions in randomly sampled plots from natural ecosystems is that the total plant biomass of the plots is expected to vary due to variation in productivity, disturbance, and so on, among the plots. Variation in total biomass due to plot heterogeneity is a likely explanation for the results reported [6], where the neighboring plants at some sites have positive (facilitative) effects and at other sites a negative (competitive) effects on the target plant. Despite this, the authors [6] concluded that the effects of competitive interactions will be averaged out at macroscales. There are many possible explanations for any static relation among neighboring plants; for example, the observation that a small plant has large neighbors. The neighbors could be large because the

subject plant is small, or the subject plant could be small because the neighbors are large. Simply put, one cannot assume that a high biomass of neighboring plants corresponds to a high competitive effect of the neighboring plants on the target plant.

Another assumption that often is used to make inferences about plant competitive mechanisms from static spatial data is to assume that the sampled plant communities are in equilibrium. A recent study [7] makes this assumption to estimate the extent of intransitive competitive interactions and their role for maintaining biodiversity in two large data sets. The authors concluded that intransitive competitive interactions are fairly common and have a positive effect on species richness. If the assumption of equilibrium is violated, then the positive effect of the estimated intransitive competition on species richness may be explained by the fact that species richness is at transient stage rather than a result of competitive hierarchies.

It is well established that few, if any, natural ecosystems are at or close to equilibrium. For some purposes, it is both mathematically convenient and useful to assume ecological equilibrium to generate predictions (with the appropriate caveats), such as assuming communities and their species abundance distributions are at equilibrium to predict extinction debt patterns over time [8]. It is more problematic to assume that plant abundances are in equilibrium in a test of the nature of the ecological mechanisms that control plant abundances, especially when we know that the test is highly sensitive to this assumption.

The Need for Dynamic Data

The notion of measuring plant competition from static spatial data is a specific case of the more general endeavor to extract ecological processes from observed patterns. New statistical methods to analyze macroecological patterns are continuously being developed. However, even the most sophisticated analyses cannot overcome the limitations of 'snapshot' data for

inferring processes: even just two points in time can produce information that simply cannot be obtained from static data.

Measuring interspecific interactions in natural ecosystems is a nontrivial task [5], and considering its ecological relevance and status as a classic question in plant population ecology, it is surprising that there have been relatively few studies that have investigated the direct effect of interspecific interactions on plant performance and their role in plant communities. The results are still too sparse to allow much generalization across different plant communities or even among years. This paradoxical situation cannot be resolved by relying on unsupported assumptions for evaluating the role of plant competition in species assembly processes.

Rather, we should focus on measuring plant growth in natural ecosystems by collecting longitudinal plant abundance data without disturbing the plant community. Several relatively labor-intensive methods of measuring plant abundance without disturbance already exist; for example, the demographic plant data analysed by Adler *et al.* [4] were extracted from digitized maps originally collected using a pantograph, and the 'point-intercept' method has been applied in several studies [5,9]. New technologies, such as LIDAR laser imaging, which can describe plants in 3D, will be game changers in the collection of species-specific longitudinal plant abundance data in natural and cultural ecosystems [10]. This will enable us to fit dynamic models of plant competition in a multitude of ecosystems and at several spatial scales.

Longitudinal plant abundance data will provide us with measures of the strength and importance of competition and allows us to predict plant community dynamics. However, if we want to understand the mechanisms that control plant competition, we need to use experiments, 'natural' experiments, human-caused 'accidental' experiments, and also long-term designed

experiment, where the uptake of limiting resources are measured [11].

Concluding Remarks

There is general agreement that there is a hierarchy of inferential power among different types of scientific data, with static patterns as the weakest, dynamic descriptive data at a higher level and controlled experiments (which are not always possible) as the strongest type of evidence. Macroecology needs to move beyond the analysis and interpretation of static ecological data sets [12]: 'It's about time.'

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