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Diversity surfaces and species wave fronts in a soil microarthropod assemblage: Adding the dimension of time

John M. Johnston*

US EPA Ecosystems Research Division, Regulatory Support Branch, 960 College Station Road, Athens, GA 30605, USA

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Summary

As a general rule, animal species of intermediate size within a given taxonomic group are most abundant in nature. It is not known if these patterns occur in small-bodied taxa, such as soil microarthropods, or how these patterns change through time. Here I show that Oribatida (Acari), the most abundant and diverse arthropod fauna of coniferous forest soils, exhibit this pattern. However, the pattern is more complex than reported for other arthropods. I analyzed the total species surface comprising 6613 individuals and 54 species by forest stand. The underlying pattern consists of 15-year stands and 30-year stands forming two distinct and separated maxima. These results suggest that assemblage patterns form early in the development of ecological communities, and that these patterns appear within the soil assemblage as waves propagating in species–abundance–body size space during forest development. These results also support the assertion that undescribed species will likely be of intermediate size within a group. This analysis contributes to investigations of biodiversity and body size relationships by adding the temporal dimension. Potential applications are in disturbance and indicator studies or other work where changes in assemblage structure are used as measures of disturbance or as response variables in manipulative studies.
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Introduction

A central problem in ecology and for the environmental sciences in general is that of scaling (O'Neill et al., 1986). That is how can the data gathered of individual organisms be aggregated to

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*Corresponding author. Tel.: +1 706 355 8300; fax: +1 706 355 8302.
E-mail address: johnston.johnm@epa.gov.

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larger scales of spatial resolution (Levin, 1991). Ultimately fine-scale data must be grouped in some manner, and individuals can be categorized taxonomically, functionally, etc. (Levin, 1991). The challenge is to group these measurements in a manner that is meaningful at a higher level of organization, while retaining relevant information from the smaller scales. This study investigates patterns of individual species within the context of forest stand development.

Diversity statistics in and of themselves are an incomplete treatment of individual phenomena. With these methods one is concerned solely with measuring diversity as the number of species in a sample. As Cousins (1991) pointed out, this is an ironic treatment of diversity. Species are separated based on established taxonomic distinctions only to be treated equally in the final calculation. In fact, body size (one of many relevant biological variables) was forsaken by conventional diversity methods (Taylor, 1978). Thus, when an index value is calculated, an implicit assumption is that all of the individuals in the equation are of comparable body size. Taylor (1978) reiterated this point with the explanation that size is eliminated from biomass by using "*N*," the number of individuals in a sample, as a measure of biomass that is in essence size-corrected.

Equal body size may be a poor assumption for many groups of organisms. For example, the size range of the adult Oribatids in this study was almost one order of magnitude. Though it is not known how the violation of the assumption of comparable body size affects the interpretation of the results when diversity indices are calculated, it should not be ignored. Energy utilization and the nature of interspecific interactions will likely differ within this range of body size (Harvey and Godfray, 1987; Cousins, 1989). Physical changes to the environment, such as soil compaction and textural changes from erosion, as well as chemical changes like nutrient availability and the presence of pesticides are also likely to affect organisms of varying body size differently. These issues concern any index or model that involves a uniform body size assumption.

A remaining difficulty with the overall integration of ecological research has been the contrast between the population–community and process—functional perspectives (Kempton, 1979; O'Neill et al., 1986). A related challenge involves the need to integrate multiple scales of observation while explaining observation sets in both space and time (Kempton, 1979; O'Neill et al., 1986; Allen and Hoekstra, 1992; Brown, 1995). Many of the early models created to test our understanding of the structure and function of ecological systems were from the process–functional point of view, and these were also non-spatial point models. Implicit in this conception of a system is that the properties of individual organisms can be neglected. This perspective seems to have shifted relatively recently, so that there is more emphasis on individual-based models, including size- and age-structured populations, and how these variables influence the outcome of the processes that are described (Jorgensen, 1993). The properties of individuals do indeed matter, and these characteristics are fundamental to our understanding of system behavior. That the sizes of organisms in our model compartments have relevance, or that body size affects the way that organisms perceive their environment, interact with other organisms, and utilize matter and energy are relevant topics for consideration. System fluxes of energy and material do not occur independent of the species involved.

Due to the interrelationship between body size, diversity and population density, it has been suggested that knowledge of the relationships between any two pairs of variables enables prediction of the third (Harvey and Lawton, 1986). Others have examined these variables in different biomes and animal communities (Morse et al., 1988; Siemann et al., 1996). Kampichler (1999) analyzed the body size–biomass distribution of both oribatids and collembola in soil cores for fractal relationships that link habitat complexity to body sizes that fit the available habitat. However, important questions remain, particularly with respect to soil fauna. Are these relationships consistent through various phases of soil assemblage development? Are patterns of species, abundance and body size consistent across different forest plots for comparative purposes? I investigated the data by forest stand using the biota as a discriminant between closely related stands. This enabled me to examine the relationships of species richness, body size and number of individuals that correspond to different phases of forest stand regeneration.

Materials and methods

The study design consisted of three pairs of soil type and age-matched (planted) stands of Loblolly pine (*Pinus taeda* L.) at the Savannah River Site, South Carolina. I sampled microarthropods monthly throughout 1991 by retrieving litterbags from each of the six forests and determined the abundance and lengths of each species of oribatid mite. The experimental stands are paired age classes that