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What is Ecosystem Structure?

RANDALL W. MYSTER

Institute for Tropical Ecosystem Studies, University of Puerto Rico, PO Box 363682, San Juan, Puerto Rico 00936. rmyster@upracd.upr.clu.edu

Ecosystems were originally defined as units of the earth's surface, that is the whole system including the organisms and the physical factors that form the environment (Tansley, 1935). As the study of ecosystem ecology evolved, ecosystems came to be categorized by their function and structure (Odum, 1953) with an emphasis on integration and indirect interaction (Muller, 1997). Ecosystem scientists divided into two camps: those concerned with measuring an ecosystem's input and output relations (flows of matter and energy; Evans, 1956) and those concerned with specific populations (Levin, 1976). However, populations reacted to stimuli from the environment, not the inverse (Allee et al., 1949; McIntosh, 1985), so that now ecosystems are seen as defined first by the biota and second by the environment (Chapin et al., 1997). Consequently, ecosystems can logically be defined as a collection of dynamic, largely stochastically occurring (Gleason, 1926), individualistically responding (Myster and Pickett, 1988) and weakly interacting (Myster and Pickett, 1992b) species and those aspects of the abiotic environment to which they respond.

I suggest that these two "camps" or traditional approaches to ecosystem function and structure (the abiotic and the biotic) can be synthesized by looking at functions that are primarily plant-based (Hooper and Vitousek, 1997) because plants (1) conduct the vast majority of an ecosystem's energy and nutrient processing (Grime, 1997), especially in the tropics where most nutrients are in the plant biomass and form loops through decomposition and uptake with relatively small inputs and outputs of nutrients in and out of the ecosystem (although there is an increasing time lag in decomposition and nutrient buildup in dead organic matter with increasing latitude; Vitousek and Sanford, 1986), (2) comprise the bulk of the biomass in ecosystems, more than any other taxon, and biomass dynamics is a key issue (Walker, 1992) and (3) may even control nutrient availability (Wedin and Tilman, 1990).

It is likely, then, that the primarily plant-based functions of productivity/respiration (the biomass build-up function) and decomposition (the biomass breakdown function; Watt, 1947) are the most critical ecosystem functions (with soil microbe [e.g., bacteria, fungi, insects] diversity and abundance also critical factors for decomposition). Furthermore, because plants must be established in order to function and, because of the individualistic nature of succession and communities, productivity and decomposition should be examined at the individual plant level (perhaps focusing on the dominant species; Mueller-Dombois, 1988). After productivity and decomposition, the next most important ecosystem functions would naturally be those aspects of energy transfer/loss and nutrient cycling that are not directly included in the plant biomass processes of productivity and decomposition.

In any ecosystem, patterns of organization at almost any spatial or temporal scale are common (Mueller-Dombois, 1988). For example, spatial distribution of tree seeds and saplings during old field succession (Myster and Pickett, 1992a) is obviously not random. However, are we justified in calling these spatial distributions, or any other organizational patterns, structure? Is there a criterion that a pattern must satisfy before it is also ecosystem structure? I suggest that, first and most importantly, structural pattern must be tied to those functions that are critical for the continued operation of the ecosystem. Further, because ecosystem structure should derive from ecosystem function (Odum, 1953) and because structure can be reasonably defined as that minimal or parsimonious pattern of organization necessary for a function to operate (similar to information theory; Muller, 1997), Table 1 offers suggestions, derived mainly from terrestrial experience, as to what those structures might be for given ecosystem functions. This linking of ecosystem structure with its corresponding function should be addressed more often and, if linkages are not found, that should be taken as evidence of nonessential or even meaningless structure.

In fact, there may be many things that are measured routinely in an ecosystem which seem to have little or no relationship to functions and therefore are questionable. Table 1 lists some common examples under category 3 (many of them "higher-order" structures not derived from individual plants or single aspects of energy/nutrient cycles; see also Muller, 1997). In these cases, the scientists investigating these structures are responsible for demonstrating the functional relationships and to argue their meaning. This framework suggests that ecosystem structure becomes more meaningful as it becomes tied to function and as that function becomes more plant-based (i.e., moves up Table 1). Although function and structure are naturally interwined, the framework shows a way to distinguish between direct and indirect relationships and could help to clarify much of the semantic confusion concerning their meaning. The case against category 3 "structures" is three-fold: (1) it is often not clear which function or process the structures have influence on, (2) any influence is likely to be indirect at best (Muller, 1997), and, (3) it is hard to determine whether such a structure is critical to a given functions operation. I suggest that we should understand ecosystem structure according to what has been clearly demonstrated over the years—that individual plant species responses, such as regeneration, growth, and decay, greatly define key ecosystem functions such as productivity and decomposition.

The functions and structures in Table 1 can be used for setting research priorities. For example, researchers could, in their ecosystem of interest containing differing species responding across key gradients and after common disturbances, (1) measure variation in rate and nutrient composition of plant productivity and decomposition, (2) model those responses, (3) measure plant structures and other energy/nutrient structures as suggested in Table 1 categories 1 and 2, (4) manipulate plant structures experimentally and measure plant functional responses and (5) explore the succession mechanisms that determined which species were found in the ecosystem. Alternatively, I suggest that researchers who focus on structures from Table 1 category 3 may discover, at best,

TABLE 1. Importance ranking of ecosystem functions with candidates for their corresponding ecosystem structures. Although the highest level functions and structures derive mainly from plants, some aspects of the table have other sources.

Ecosystem function	Possible ecosystem structures
(1) Productivity	plant specific leaf area plant gas exchange structures plant root to shoot ratio plant leaf/stem architecture canopy structure/leaf area index nutrient use efficiency
Decomposition	plant tissue chemistry soil biota
(2) Energy transfer/loss	food web length/complexity/connectivity
Nutrient/water cycling	soil chemistry soil density/composition atmospheric deposition/weathering watersheds/leaching/transpiration food web length/complexity/connectivity
(3) ???	stability/resiliency/homeostasis niche breadth/overlap species competitive hierarchies self-organization/regulation/entropy

only indirect links to the key ecosystem functions of productivity, decomposition, nutrient cycling, and energy capture/transfer/loss.

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