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ScienceDirect
Geomorphology 89 (2007) 111 – 126
GEOMORPHOLOGY
www.elsevier.com/locate/geomorph

The problem of boundaries in defining ecosystems: A potential landmine for uniting geomorphology and ecology

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Received 10 March 2005; received in revised form 27 July 2006; accepted 27 July 2006
Available online 25 September 2006

Abstract

Forging stronger linkages between geomorphology and ecosystem ecology depends, in part, upon developing common conceptualizations of an ecosystem. Because most ecosystem processes are scale dependent, the choice of boundaries is of profound importance to the conceptualization of an ecosystem and to the scope and validity of questions being asked within that ecosystem. Indeed, any conceptualization of an ecosystem requires constraining the spatial and temporal scales of analysis. Thus, it is of particular importance to match the ecosystem boundaries to the question being asked or to the processes being studied and, to facilitate better communication among disciplines, to be explicit in the definitions adopted for an ecosystem.

Defining an ecosystem can be problematic when the processes of interest operate at potentially different scales, and little research exists comparing scales of geomorphic processes with those of ecological processes. Here we will discuss the importance of scale in geomorphic and ecological research, and compare and contrast disciplinary biases and inclinations. To highlight the problem of conflicting spatial scales, we will draw on recent attempts to link the structure of food webs to measures of ecosystem size. In particular, problems arise where little or no strong association exists among community membership, resource supply, and physical boundaries. Similar problems arise when trying to link geomorphologic and ecological processes that can operate at different, but variable, temporal scales.

Keywords: Ecosystem; Food web; Boundary; Food chain length; Spatial scale; Temporal scale; Resource subsidies; Community membership

1. Introduction

One can "*…define ecosystems as the smallest units that can sustain life in isolation from all but atmospheric surroundings. However, one is still left with the problem of specifying the area that should be included.*"

O'Neill et al. (1986)

The "ecosystem" is an appealing and important concept in ecology. Tansley (1934) introduced the concept of an ecosystem as "the whole system (in the sense of physics), including not only the organism-complex, but also the whole complex of physical factors forming what we call the environment of the biome." At its core, the ecosystem is a place where organisms and the environment interact. This conceptualization of an ecosystem is fine for introductory textbooks, but is, perhaps, too broad to provide a working definition of an

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doi:10.1016/j.geomorph.2006.07.014

ecosystem. On the other hand, simple definitions – a lake, a stream, an old field – based on easily identified physical boundaries, while practically appealing, can create problems when they fail to adequately address the complexity of natural systems within the question being addressed. Difficulties in defining the boundaries of an ecosystem are of concern where highly mobile organisms and constituents interact at multiple spatial and temporal scales. This is particularly important where the dynamics of systems are determined by interactions across multiple levels of the biological hierarchy (e.g., where population dynamics determine nutrient cycling). While some authors suggest ecosystems are a fundamental unit of study for ecology (Golley, 1993), others disparage ecosystems as fuzzy human constructs. This discourse is not unique to ecosystems; it is pervasive in ecology and evolutionary biology because it applies to all human constructs including species (Hey, 2001; Hey et al., 2003), populations (Berryman, 2002; Camus and Lima, 2002), and communities (Root, 1973; Allen and Hoekstra, 1992).

Ecosystem processes are scale dependent and, as such, the choice of boundaries for an ecosystem is of profound importance to the conceptualization of an ecosystem and the scope and validity of questions being asked within that ecosystem (O'Neill et al., 1986). Indeed, any conceptualization of an ecosystem for theoretical or empirical studies requires constraining the spatial and temporal scales of analysis (even implicitly), such that ecosystem boundaries match the question being asked or process being studied. For many questions, definitions of ecosystem size are relatively straightforward. For example, efforts to estimate primary production in a lake or nitrogen spiraling in a stream are relatively well-bounded because they refer to processes dominantly bounded by the physical boundaries of the system under study. In contrast, defining an ecosystem is more problematic when the processes of interest operate at potentially different scales. For example, if annual patterns of primary production and nutrient cycling in a stream reach are strongly influenced by marine subsidies borne by anadromous fish, the local ecosystem properties are likely strongly influenced by marine community structure through the effects on the dynamics of fish populations.. In this latter case, the answer to the question posed depends critically upon the definition of the size of the ecosystem, but the scale of the ecosystem is not clearly defined because little or no strong association occurs among community membership, resource supply, and physical boundaries. This is often the case for questions relating to the structure of food web to ecosystem processes because they link the dual nature of, or approaches to, ecosystems, which O'Neill et al. (1986) have classified as the population–community and process–function approaches.

We raise the issue of ecosystem boundaries in this context because (i) a common conceptualization of ecosystems is essential for forging stronger linkages between geomorphology and ecosystem ecology, (ii) many ecosystem boundaries are shaped by geomorphic processes, and (iii) surprisingly little research exists comparing the scale of geomorphic and ecological processes. This topic is also of interest to us because of its central role in much of our research on the structure of the food web and ecosystem function in aquatic ecosystems. Here, we discuss some of the issues and pitfalls of spatial and temporal scales in geomorphic and ecological research, and compare and contrast disciplinary biases and inclinations. In this context, we discuss the dual nature of ecosystems and use our research on the structure of the food web and ecosystem function in streams to explore some of the more difficult issues surrounding definitions of ecosystem boundaries.

2. The dual nature of ecosystems

We raise the dual nature of ecosystems to set the context for understanding what we perceive as some of the more difficult scaling issues in ecosystem ecology and geomorphology. Following O'Neill et al. (1986), we will exaggerate the differences between the population–community and process–function approaches to highlight our point. Neither approach is inherently correct; rather, each is appropriate for representing one aspect of the dual nature of ecosystems. Problems arise in scaling when the two approaches collide, such as they often do in food web ecology. Here, we offer only a brief thumbnail sketch of these two approaches. A full discussion of these approaches and implications for ecology can be found in O'Neill et al. (1986). These approaches have parallels in geomorphology in the contrast between landscape-level landform studies and more mechanistic process-based approaches, thus mirroring the population–community and process–function approaches, respectively.

2.1. The population–community approach

This approach views ecosystems as a network of interacting populations that reside within or upon an abiotic template that is the environment (O'Neill et al., 1986). Here species, populations and communities are dominant entities (including the classic connectance food webs) that are shaped by processes such as