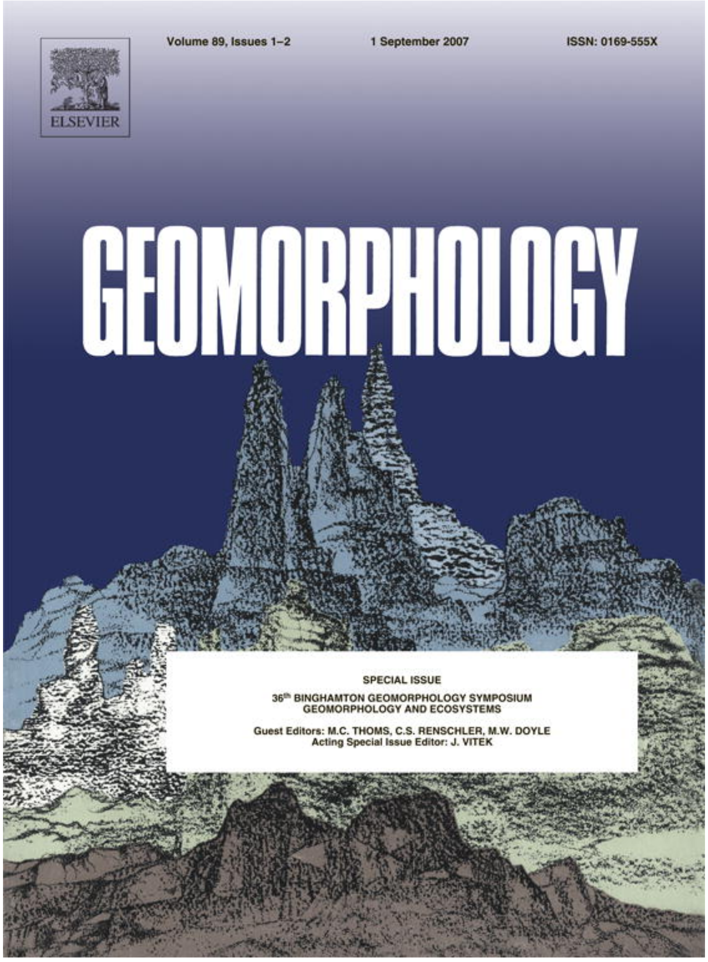
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The problem of boundaries in defining ecosystems: A potential landmine for uniting geomorphology and ecology

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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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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 population growth, predation, competition, and, ultimately, evolution. The entangled bank so elegantly outlined by Darwin (1859) is a natural analogy for this approach, where the focus of most questions is clearly on the organism. Spatial and temporal scales of analysis are typically based on organismal traits such as generation time, migration routes, and home range size, and are often easy to grasp because they relate to the human scale of perception (O'Neill et al., 1986).

In linking geomorphology and ecology, the bulk of previous studies have focused on how geomorphology influences ecosystems within this research approach, e.g., the effect of particular geomorphic forms or processes on vegetation communities or fish populations. For instance, one of the most widely cited linkages between geomorphology and ecology, the River Continuum Concept (Vannote et al., 1980) describes how systematic downstream changes in the river channel geometry drive commensurate spatial changes in the community composition of the stream biota. Spatial scales of geomorphic variability roughly match those of biotic community composition, and so conceptually linking geomorphic forms to community composition is inherently convenient. While the River Continuum Concept links geomorphology and biotic communities at roughly consistent spatial scales, other studies link geomorphology and biotic communities at consistent temporal scales, noting the coupled dynamic adjustability of biotic communities as driven by geomorphic changes. For example, Hupp (1992) linked predictable temporal changes in riparian vegetation communities to systematic temporal changes in river channel geomorphology. Furthermore, Hupp (1992) showed how these vegetation changes served as powerful feedbacks from the biota to control future geomorphic processes. Linking geomorphic forms and processes to population–community ecology is prevalent in the literature, and is because the spatial and temporal scales of variability are comparable. The feedbacks from geomorphology to ecology, and vice-versa, are often evident and, thus, of interest to both disciplines (e.g., Hupp, 1992).

2.2. The process–function approach

This approach focuses on processes that influence the flux and flow of energy and material through an ecosystem (O'Neill et al., 1986). Instead of focusing on organisms, the process–function approach addresses the functional role of constituent parts of ecosystems and, therefore, is often organized around understanding the cyclic causal pathways (e.g., Hutchinson, 1948) that maintain ecosystem functions. Energy flow (Lindeman, 1942; Odum, 1957) and biogeochemistry (Likens, 2001) are points of focus for ecosystem ecology under this approach. At one extreme, this approach uses "black box" approaches to measure inputs and outputs of material or energy through an ecosystem, and implies that energy flow or nutrient cycling are more important than the identity of the organisms performing these functions. Most contemporary studies recognize that biotic and abiotic components of an ecosystem are intimately linked and that the behavior of organisms and species identity matter (Jones and Lawton, 1995). Spatial and temporal scales are diverse, ranging from long-term "whole ecosystem" studies to process-based studies of limited spatiotemporal extent, such as studying the rates of leaf decomposition in streams.

In contrast to the population–community approach, studies are lacking that attempt to link geomorphology to ecosystems via the process–function approach. Two potential explanations exist for this lack of collaboration. First, while geomorphic influences on ecosystem process–functions are potentially strong (e.g., Alexander et al., 2000), the feedbacks from ecology to geomorphology are not evident, and, thus, potentially of lesser research interest to geomorphologists. In addition, the scales of geomorphic forms and the subsequent ecosystem processes are profoundly different (channel reach scale compared to microbial processing of nutrients), and, thus, impose difficulties on the logistics of coupled studies. We return to linking geomorphology and ecosystem processes below.

2.3. Implications

At a fundamental level, these two approaches represent the dual nature of ecology, and the difficulties of linking geomorphology to each of these approaches. They also provide us with a useful definition of an ecosystem — a region of strong interactions among organisms and between organisms and the flux and flow of energy or material. Many studies avoid problems with scale either by working entirely within one of these approaches, or by working in systems where the scale of analysis for these two approaches is similar (see section below on well-bounded ecosystems). It is the question that operates across both approaches in which problems of scale become most difficult to resolve because the question being asked may not set the scale of analysis. This is where problems with integrating geomorphology and ecosystem ecology are likely to emerge most strongly. For example, geomorphological processes that shape channel morphology regulate local hydrology and nutrient cycling at small (Stanley and Doyle, 2002) and large (Alexander et al., 2000) spatial scales, but may not operate at the same scales as those that shape the evolution of organisms and their interactions (Montgomery, 2000). Food web ecology emerges from both approaches, yet all too often food webs are considered exclusively from one of the approaches. Unfortunately, as we will highlight below, major problems with delineating ecosystem boundaries emerge when approaching food web questions from both the population–community and process–function perspectives.

3. Defining ecosystem boundaries

Boundaries have been defined in a variety of ways by ecologists (Puth and Wilson, 2001; Wiens, 2002; Strayer et al., 2003; Table 1). Generally, boundaries are defined based on either physical or functional criteria. Key attributes include the relationship between the boundary and the process being studied, the origin of the boundary, and the form of activities taking place along the boundary, which is a function of permeability (Strayer et al., 2003; Table 1). Other important characteristics might include grain, extent, and dimensionality, all of which can be particularly important for landscape studies of structural boundaries (Strayer et al., 2003).

Physical or structural criteria are the basis of the "tangible" boundaries traditionally recognized by landscape ecology (Puth and Wilson, 2001; Wiens, 2002; Strayer et al., 2003). Structural boundaries are typically based on visible or measurable discontinuities at physical boundaries (e.g., aquatic–terrestrial) or changes in the biotic composition of two habitats (e.g., shifts in dominant plant species; Table 1). The aquatic–terrestrial boundaries dividing rivers and riparian zones, freshwater lakes and terrestrial catchments, and oceans and oceanic islands are all pervasive and visible ecosystem boundaries based on structural characteristics of the landscape. Despite the widespread use of physical structure-based boundaries (Strayer et al., 2003), these "tangible" boundaries can prove misleading when they do not map onto the ecological processes of interest (Puth and Wilson, 2001). In other cases, structural and functional boundaries are congruous, making these tangible boundaries extremely useful for ecological studies.

Table 1
Attributes of boundaries

Types of definition:	
Structural	Based on physical boundaries (e.g., watersheds, aquatic–terrestrial)
Functional	Based on changes in the rates of interactions and exchanges among units of study
Relationship to process of interest:	
Structural	Structural boundaries can be process-independent
Functional	By definition, functional boundaries depend upon the process of interest
Origin:	
Structural:	
Geomorphic	Topographical boundaries including watersheds, aquatic–terrestrial boundaries, continental shelf vs. deep sea, etc.
Physiochemical	Thermoclines and chemoclines, e.g., freshwater–saltwater boundaries in estuaries.
Dimensional	Surface-related boundaries including surface vs. soil, benthic vs. pelagic, ground vs. canopy.
Biological	Physical boundaries among habitats, e.g., the boundary between old fields and forest.
Functional:	
Material and energy flow	Ecosystem boundaries defined by steep gradients in the flow of material and energy including resource sheds, nutrient spiraling, and discontinuities in nutrient or energy exchange. Often mediated by structural boundaries that limit exchange between ecosystems.
Species interactions	Community boundaries defined by the location of weak(er) species interactions. At times mediated by structural boundaries that limit interactions among species.
Movement of organisms	Population boundaries set by limits to immigration or emigration, and gene flow. Often mediated by structural boundaries that limit migration and gene flow.
Activities:	
Transmission	The boundary is semi-permeable and allows only a fraction of organisms or material to pass, or reduces the strength of species interaction.
Transformation	The boundary changes the state of material or species interactions, e.g., N transformation at the soil–stream interface.
Absorption or reflection	The boundary is impermeable and either stops or redirects interactions among species or the flow of organisms and material.
Neutral	The boundary does not affect the flow of material or species interactions. Can only apply to structural boundaries.

Functional definitions of boundaries revolve around the ability of boundaries to mediate interactions and exchanges among units of study (e.g., ecosystems, communities, populations, habitat patches, watersheds; Puth and Wilson, 2001; Wiens, 2002) and are central to defining ecosystems. The population–community and process–function approaches both provide guidance for defining more functionally appropriate boundaries of an ecosystem, although linking the two approaches is made difficult in "open" ecosystems where ecosystem processes often operate at very different scales (more on this below). For questions imbedded within the process–function approach to ecology, ecosystem boundaries are probably best set by discontinuities or steep gradients in the flux and flow of material and energy (Allen and Hoekstra, 1992; Power and Rainey, 2000; Likens, 2001), or by discontinuities or steep gradients in the physical parameters that drive these fluxes (Fisher et al., 2004). For questions revolving around interactions among organisms and emerging from the population–community approach, community membership and ecosystem boundaries are typically best set by discontinuities or steep gradients in species interactions (Root, 1973; Allen and Hoekstra, 1992). Similar arguments can be made for populations, such that populations are defined by gradients in rates of immigration and emigration (e.g., see Berryman, 2002; Camus and Lima, 2002). All of these boundaries are set by the functional role in ecosystem and community processes (Puth and Wilson, 2001; Cadenasso et al., 2003a) and can be detected using statistical techniques (Cadenasso et al., 2003b; Fagan et al., 2003). In many cases these boundaries will be strongly governed by geomorphic forms or processes (e.g., Power and Dietrich, 2002; Fisher et al., 2004), while in other cases ecosystem boundaries may be somewhat independent of the physical landscape.

3.1. Well-bounded systems

Where strong associations occur among resource flow, community membership and physical boundaries, which is common for lakes and islands, delineating ecosystem boundaries is relatively straightforward because of the convergence of functional and structural attributes of those boundaries (Fig. 1). These systems are commonly viewed as ecosystems because they are *well-bounded*. Our use of well-bounded for these systems is intentional — we do not want to imply that these systems are closed. Instead, interactions among organisms are typically stronger and cycling of material and energy is typically tighter within than across the physical boundaries of these ecosystems. The physical or geomorphic forms that provide the structural boundaries make exchange of organisms or resources into and out of these ecosystems difficult, or at least minor in comparison to exchange within the boundaries. In well-bounded ecosystems, often a one-to-one mapping of populations, communities, and ecosystems occurs, such that multiple processes and mechanisms all operate at the same general spatial scale. These systems are ideal for studying interactions among population dynamics, community structure, and ecosystem function (e.g., Forbes, 1887; Hutchinson, 1964; Carpenter et al., 1987) because they provide a common spatial scale for analysis. Furthermore, they provide convenient systems for studying geomorphic–ecological linkages because causal relationships between physical forms or processes and biotic responses become evident.

3.2. Open systems

In contrast to well-bounded ecosystems, a myriad of more physically open systems exist, including most terrestrial habitats, estuaries, and streams, for which

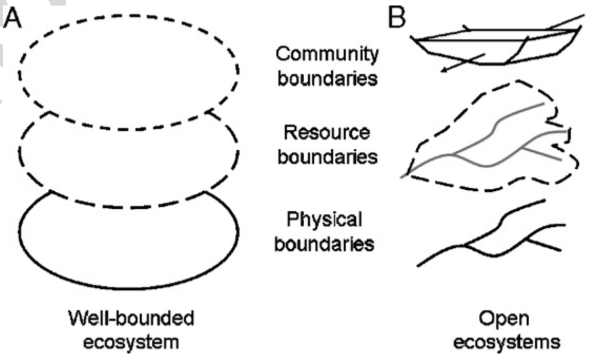

Fig. 1. Spatial correspondence among physical boundaries, community boundaries, and boundaries of the resource shed in well-bounded and open ecosystems. In well-bounded ecosystems (A), a strong spatial correspondence occurs among all three sets of boundaries, for example at the aquatic–terrestrial boundaries of many lakes or islands. In open ecosystems (B), little correspondence exists among boundaries. Our example of an open ecosystem is a stream where community interactions are realized at the local reach scale, the resource shed includes upstream reaches of the stream and most of the watershed, and the physical boundaries of the ecosystem include the entire stream system.

boundaries are anything but clear. Boundary problems are prevalent in these systems both because they are not fully delineated by well-defined physical boundaries and because little congruence exists among the physical boundaries (where they exist), community membership, and ecosystem processes (Fig. 1). Thus, the functional role and structural attributes of ecosystem boundaries are segregated, and different processes and mechanisms often operate at very different spatial scales. In open systems an explicit statement of spatial scale is most important because the question of interest typically determines the proper scale of analysis.

A number of solutions to the lack of physical boundaries have been proposed, but none provide a solution that integrates both approaches to ecosystems. For example, Cousins (1990) proposed the "ecotrophic module," defined by the foraging area, home range, or population range of top predators in the food web, as useful for delineating the spatial boundaries of an ecosystem. Cousins' framework is similar to that for sink food webs (sensu Cohen, 1978), where membership is defined as the prey of a top consumer, and the prey of the prey of the top consumer, and so on until the basal resources are reached (see also Holt, 1996). Cousins' framework is appropriate for and solves many of the boundary problems with the population–community approach in open ecosystems. It is not, however, sufficient to address boundary issues related to the flux and flow of energy and material across the landscape. Power and Rainey (2000) proposed the use of resource sheds as a useful delineation of ecosystems. In open systems, Power and Rainey (2000) suggest that boundaries to the resource shed might be related to the joint probability of a given resource being assimilated by an organism or returned to the environment by an organisms. This corresponds closely to our definition of ecosystem boundaries as being set by discontinuities or steep gradients in the flux and flow of material and energy. Each definition (Cousins, 1990; Power and Rainey, 2000) provides a powerful perspective for dealing with community interactions or resource dynamics in open ecosystems; however, on their own, neither is sufficient to simultaneously deal with highly mobile organisms and multiple resources because they often operate at different spatial scales in open systems. Typically, different definitions of ecosystem boundaries will be required for addressing different questions in open ecosystems.

3.3. Subsidized ecosystems

This brings us to the explicit consideration of subsidized ecosystems. Good and growing examples exist of the open nature of what appear to be, at first glance, well-bounded ecosystems. Polis and colleagues working on islands (Polis and Hurd, 1995; Polis and Hurd, 1996; Polis et al., 1997), and since then many researchers in various habitats (e.g., Post et al., 1998; Nakano and Murakami, 2001; Sabo and Power, 2002), have documented the importance of spatial subsidies (e.g., allochthonous inputs) on the dynamics of the food web and ecosystem function. As we noted earlier, all ecosystems are open to some flows of energy, material, and organisms (Polis et al., 1997), particularly at longer time scales, but when these inputs are large at short temporal scales, they strongly impact our thinking about boundaries.

Spatial subsidies are of particular importance to our thinking about boundaries in systems, such as lakes and islands, with clear physical boundaries that provide the appearance of well-bounded systems but where spatial subsidies of resources or organisms disrupt the congruence between physical boundaries, ecosystem processes, and community membership. Where highly mobile organisms, such as geese (Post et al., 1998; Kitchell et al., 1999) and fishes (e.g., Donaldson, 1969; Durbin et al., 1979; Winemiller and Jepsen, 1998), move large amount of nutrients around the landscape, the lakes, wetlands, and streams receiving these nutrients are spatially linked or embedded within a functionally much larger ecosystem. For example, snow geese in New Mexico, moving nutrients from agricultural fields where they feed to wetlands where they roost, supply 40% of the nitrogen and 75% of the phosphorus to their roosting wetlands during winter months (Post et al., 1998). In these systems, the dynamics of nutrients in local wetlands are linked to regional agricultural systems at short time scale by the daily migration of geese, and linked to the entire migratory range of geese at annual and decadal time scales by seasonal migrations (Jefferies, 2000). Similarly, where anadromous fishes are important sources of nutrients to lakes and streams, climate change, harvesting, and complex trophic interactions in marine systems hundreds or thousands of miles away can strongly influence local nutrient dynamics (Finney et al., 2000; Power and Rainey, 2000). Finally, where highly mobile predators, such as piscivorous birds, have strong impacts on local structure of the food web (Power et al., 1989; Polis et al., 1997), local dynamics will be a function of processes operating at much greater spatial scales (Holt, 1993; Holt, 1996; Holt, 2002) — this is the basis of some of the contemporary work on metacommunities (e.g., Cottenie et al., 2003; Mouquet and Loreau, 2003; Leibold et al., 2004).

Spatial subsidies break apart the congruence of geomorphic–biotic ecosystem boundaries when the inputs overwhelm local dynamics. Spatial subsidies driven by passive diffusion or local movement will be most important in systems where perimeter-to-area (P/A) or surface-area-to-volume ratios are high (Polis and Hurd, 1996; Polis et al., 1997). All else being equal, small ecosystems with high P/A ratios are likely to be most strongly influenced by spatial subsidies (Cole et al., 1990; Polis and Hurd, 1996; Schindler and Scheuerell, 2002). Likewise, the importance of spatial subsidies driven by vectors or moving through corridors for which surface area is not relevant (Puth and Wilson, 2001), should be influenced by the size of the local system (or more precisely the state of the local system — e.g., phosphorus concentration of prey population size) and the magnitude of the subsidy. For example, with anadromous fishes acting as nutrient vectors, geology, geomorphology, and watershed size can all influence the availability of nutrients in a watershed, while the population size of anadromous fishes influences the magnitude of input. Large watersheds with few anadromous fishes may be effectively well-bounded, while the same number of fish may overwhelm the nutrient dynamics of small watersheds, rendering them functionally *open* ecosystems. Likewise, the same amount of nutrients borne by anadromous fishes will have a greater impact on local nutrient dynamics in low productivity ecosystems than in higher productivity ecosystems (often a function of local geology).

3.4. Watersheds

Watersheds and streams are well-studied examples that represent inherent challenges to integrating ecology and geomorphology. Watershed boundaries, determined by long-term geomorphic processes, are set by discontinuities in the flow pathways of water and the material carried downstream by water (Likens, 2001), and are the ecosystem unit most commonly shared between ecology and geomorphology. Watersheds are an important and successful unit for studying terrestrial ecosystem processes (e.g., Hubbard Brook; Likens et al., 1977; Hedin et al., 1995; Likens, 2004) and stream ecology (Stoddard, 1994; Power et al., 1995a,b; Harding et al., 1998; Power and Rainey, 2000; Power and Dietrich, 2002; Sabo and Power, 2002), which is heavily influenced by watershed-scale processes. Watershed boundaries are, however, open to numerous processes, among which the migration of birds or anadromous fishes are the most apparent, and are not, therefore, appropriate for many questions in ecology.

Watersheds are powerful tools for terrestrial ecosystem ecology, where there is strong correspondence among the spatial scales of investigation, physical boundaries to material flow, and the geomorphic and ecological processes of interest (e.g. watershed scale nutrient biogeochemistry, and analogous studies of sediment flux; Likens, 2001). In this context, the watershed isolates a unit of study where internal cycling is stronger than external inputs (Likens, 2001), again mirroring our definition of an ecosystem based on the process–function approach. Thus, two substantial advantages exist to using the watershed as an ecosystem boundary. First, the watershed approach emerges from the strong linkage between the movement of material or energy and the movement of water, allowing the physical boundaries of watersheds to be strongly linked to the functions of interest. In this context, geomorphology has strong impacts on ecological processes. For example, watershed slope and riparian zone geomorphology are important variables in watershed form and can mediate the loss of nutrients and carbon, although problems of heterogeneity, the identification of mechanism, and a simplistic view of geomorphology remain problematic (Likens, 2001). The second advantage of the watershed is that fluvial geomorphology is, obviously, studied primarily within a watershed context, and so predictive models, conceptual and numerical, are available for many geomorphic processes that occur at and within the watershed scale. As geomorphic processes are linked to ecosystem processes, these geomorphic models can enhance our ability to make predictions of how ecosystems should systematically vary through space and time at the watershed scale (e.g., Vannote et al., 1980; Alexander et al., 2000).

Stream ecology has made enormous progress in integrating a geomorphic perspective (geomorphic forces are implicit in all of stream ecology), and a number of comparative and mechanistic studies have considered how geomorphology might influence interactions of the food web (Power et al., 1995a,b). Yet, much of the integration of geomorphology into stream ecology has been, perhaps, a bit superficial because it primarily viewed geomorphology as a static property of stream ecosystems (Fisher et al., 2004). This is, in part, an issue of temporal scales. Many ecological processes occur over relatively short temporal scales (e.g., within a modern temporal scale for geomorphology; *sensu* Schumm and Lichty, 1965) and as such geomorphology can often be considered constant. This assumption breaks down, however, where ecological processes occur over very long time frames (e.g., speciation; Montgomery, 2000) or where geomorphic changes occur rapidly (e.g., dam removal, Power et al., 1996a; Doyle et al., 2002; Stanley and Doyle, 2002; Doyle et al., 2003a).

3.5. Space and time

Space and time are intimately linked in any discussion of boundaries (Schumm and Lichty, 1965). Whether a system is open or well-bounded depends, to a great extent, on the temporal scale of analysis (Fig. 2). At relatively long temporal scales, all ecosystems are open, with external inputs and outputs overwhelming internal cycling or the colonization and extinction of organisms dominating community interactions. Likewise, many physically open ecosystems can be treated as well-bounded at short temporal scales (Fig. 2). Mean residence time (e.g., mass/flux) might provide a temporal measure of permeability of an ecosystem to the flow of material, energy, or organisms. For example, mean residence time of water or nutrients in most natural lakes, which typically scales with lake size, is on the order of years to centuries (Howarth et al., 1996). As such, annual export of nutrients is low (or its reciprocal nutrient retention is high) and, for questions about the dynamics of nutrients, these ecosystems are well-bounded at temporal scales shorter than the mean residence time but open at temporal scales longer than the mean residence time. Where phosphorous loading is increased by anthropogenic inputs or mobile organisms, residence time falls and the ecosystem is more likely to become functionally open at shorter temporal scales. In contrast, streams have much shorter mean residence times of water and nutrients (Howarth et al., 1996; Peterson et al., 2001; Gucker and Boechat, 2004; Mulholland et al., 2004) and are, therefore, well-bounded only at short temporal scales (minutes to days). For many questions about resource boundaries, tracers, such as stable isotopes, provide a powerful tool to delineate the spatial and temporal extent of boundaries (Power and Rainey, 2000). Measures of the turnover rates for organisms, rates of change in species interactions (Paine, 1980; Brown et al., 2001), or measures of gene flow can provide similar measures for population–community questions.

4. Food-chain length

Food webs provide a powerful framework for addressing questions that link population dynamics and community structure to ecosystem function because they can represent both species interactions within a community and energy flow through those species (Paine, 1980; Post, 2002a). As such, they are often imbedded with or extend across traditional ecosystem units (Holt, 1993; Polis et al., 1997). Questions about food webs emerge from both approaches of ecology. Food-chain length– a measure of the number of times energy and material are transferred from the bottom to the top of a food web – is a food web characteristic of particular importance to ecosystems because it influences community structure, species diversity, and stability by altering the organization of trophic interactions (Hairston et al., 1960; Carpenter et al., 1987; DeAngelis et al., 1989; Power, 1990; Carpenter et al., 1992; Carpenter and Kitchell, 1993; Wootton and Power, 1993; Pace et al., 1999; Persson, 1999; Schmitz et al., 2000), it modifies major ecosystem functions such as nutrient cycling, primary productivity, lake thermal properties, and atmospheric carbon exchange (Carpenter et al., 1987; Mazumder et al., 1990; Power, 1990; Elser et al., 1996; Schindler et al., 1997; Cole et al., 2000), and it partially determines the concentration of contaminants in top predators, including most of the fish humans eat (Kidd

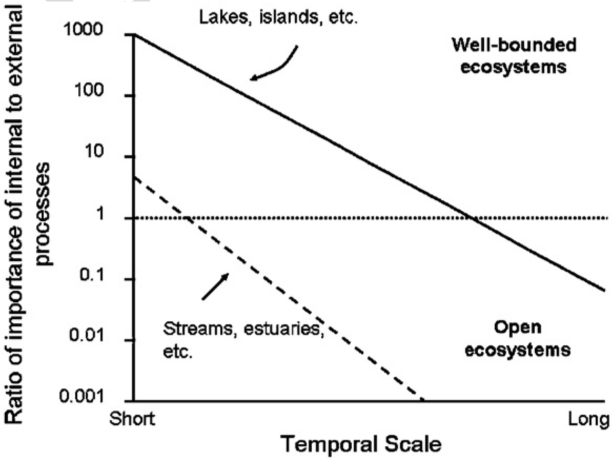

Fig. 2. Characterizing an ecosystem as well-bounded or open depends upon the temporal scale of analysis. Where the ratio of the importance of internal to external processes is high (i.e., local nutrient cycling or species interactions dominate the ecological processes), a system can be considered well-bounded. Where the ratio is low, an ecosystem would be considered open. Some systems, such as lakes and islands, might be well-bounded at short to intermediate temporal scales and open at longer temporal scales. In contrast, many more physically open ecosystems such as streams are likely to be well-bounded at only very short temporal scales.

et al., 1995; Kidd et al., 1998). Food-chain length is, arguably, the attribute of the food web most strongly affected by human activities through harvesting activities (Pauly et al., 1998; Pauly et al., 2001), habitat fragmentation (Gascon et al., 1999; Terborgh et al., 2001), and alterations of hydrology and geomorphology (Power, 1995; Power et al., 1996b; Wootton et al., 1996).

Since 1927, when Charles Elton first noted that the food-chain length was variable (Elton, 1927), ecologists have worked to document and explain variation in the food-chain length (Hutchinson, 1959; Pimm and Lawton, 1977; Pimm, 1982; Briand and Cohen, 1987; Jenkins et al., 1992; Sterner et al., 1997; Kaunzinger and Morin, 1998; Post et al., 2000; Kitching, 2001; Post, 2002a). Despite its central place in ecology, the processes controlling food-chain length remain poorly understood (Post, 2002a). Previous research has identified three factors that may strongly influence the food-chain length: ecosystem size, resource availability, and disturbance (see Pimm, 1982; Lawton, 1989; Post, 2002a for reviews). While ecosystem size and resource availability can have separate effects (Post et al., 2000; Post, 2002a), they also can be linked through joint effect on total resource availability as outlined by the productive-space hypothesis (Schoener, 1989), a recent formalization of the long standing energy-flow hypothesis which is based on the second law of thermodynamics (Hutchinson, 1959; Pimm, 1982). Schoener (1989) proposed the productive-space hypothesis to address the absence of spatial considerations for estimates of productivity or resource availability in previous versions of the energy flow hypothesis (Pimm, 1982). The productive-space hypothesis predicts that food-chain length should increase with the product of ecosystem size (area or volume) and some measure of per-unit-size productivity (e.g., g carbon m^{-2} $year^{-1}$). The productive-space hypothesis is a modern restatement of the energy flow hypothesis outlined by Hutchinson (1959) and based on the second law of thermodynamics. As originally conceived, it proposes that, because a diminishing amount of energy reaches upper trophic levels, food-chain length should increase as the amount of energy or limiting resources available to top predators increases (Lindeman, 1942; Hutchinson, 1959). The amount of resource reaching top predators is a function of resource availability at the base of the food web and energetic efficiencies throughout the food web (Pimm, 1982; Yodzis, 1984). Recent work in lakes has focused on disentangling the effects of ecosystem size and resource availability (Post et al., 2000; Post, 2002a). In streams, ecosystem size, resource availability, and disturbance may all play a role in regulating the food-chain length (Post, 2002a), and all three factors are tightly linked to the local geomorphology and strongly influenced by the delineation of ecosystem size.

4.1. Ecosystem size

The importance of ecosystem size in determining community structure has long been recognized (e.g., MacArthur and Wilson, 1967), but only recently has it been integrated clearly into the discussion of food-chain length (Schoener, 1989; Holt, 1996; Spencer and Warren, 1996; Post et al., 2000; Post, 2002a), in part because of the difficulties of defining ecosystem size in many natural systems (Cousins, 1990; Post, 2002a). Ecosystem size is important to this discourse because it may impact food-chain length (i) directly through its effect on total resource availability (i.e., productive-space hypothesis; Schoener, 1989) or, (ii) indirectly through its impact on important community characteristics, such as habitat availability, species richness, and colonization and extinction probabilities, that are independent of the direct effects of resource availability (Schoener, 1989; ecosystem-size hypothesis; Cohen and Newman, 1992; Holt, 1996; Spencer and Warren, 1996; Post et al., 2000; Post, 2002a). Because the productive-space hypothesis (point 1 above) is based on the second law of thermodynamics, it sits within the very core of the process–function approach to ecosystem ecology. Indeed, the development of the process–function approach is entangled with the development of early ideas about the structure of the food web and food-chain length (Hutchinson, 1959). On the other hand, the ecosystem-size hypothesis (point 2 above) is based on properties of the community and is associated with ideas about community assembly, island biogeography, and local species interaction (Cohen and Newman, 1992; Holt, 1996; Post et al., 2000; Post, 2002a), placing it squarely within the population–community approach. Interestingly, Elton (1927) originally suggested body size relationships among organisms were the key determinant of food-chain length, an idea consistent with the population–community approach and supported by recent analyses (Post, 2002a). Recent results from lakes do not support the productive-space hypothesis, suggesting instead that the effects of ecosystem size are independent of its effect on total resource availability (Post et al., 2000; Post, 2002a); however, it is possible that ecosystem size may govern food-chain length through its impact on total resource availability in other ecosystems such as streams (Post, 2002a).

In well-bounded systems, such as the lakes studied by Post et al. (2000), the observation that the functional role of ecosystem size spans the dual approaches to ecosystems does not cause any major problems for defining ecosystem size. In lakes, area or volume, which captures more of the vertical habitat structure in lakes than area, are appropriate measures of ecosystem size because community membership and ecosystem processes are typically contiguous with and constrained by the physical boundaries of the lake (Fig. 1a; recognizing the exceptions of small lakes where external inputs can be quite important and lakes linked to the ocean and supporting anadromous fishes).

Ecosystem size in more open systems, such as streams, becomes more difficult to define because there is often less congruence between physical boundaries and the ecological processes of interest (Fig. 1b). In streams, community interactions are typically determined by the physical boundaries of the stream itself, therefore ecosystem size for questions derived from population–community approach (O'Neill et al., 1986) might be best approximated by some measure of the cross-sectional area of the study reach at base flow, or cross-sectional area times the length of the stream over which top predators operate (e.g., a measure of home range size as was proposed by Cousins, 1990). Because cross-sectional area provides an index of the volume of available habitat, it is an appropriate measure of ecosystem size for inferring community interaction, although there may be multiple potential measures of cross-sectional area. For example, cross-sectional area measured across a pool may be an order of magnitude different than cross-sectional area measured in a riffle. Where cross-sectional area is being used as a measure of available habitat for community interactions, the cross-sectional area of the pool may better capture the habitat required to maintain top predators such as fish (Power, 1984; Power et al., 1989; Finlay et al., 2002). Resource availability in streams, because of the high perimeter-to-area ratio, is typically determined by allochthonous inputs (Wetzel, 1992; Wallace et al., 1999; Nakano and Murakami, 2001; Power, 2001; Naiman et al., 2002; Sabo and Power, 2002; Sabo and Power, 2003), and ecosystem size may be best approximated by catchment or watershed area (or other measures of the resource shed; Power and Rainey, 2000). For many questions, the resource shed closely approximates the boundaries expected for questions from the process–function approach to ecology (O'Neill et al., 1986). On the other hand, while most streams are net heterotrophic, growing evidence exists that, in all but the smallest streams, upper trophic levels are largely supported by *in situ* algal production (Finlay, 2001; Thorp and Delong, 2002), which could present some real challenges for delineating just the resource shed (Power and Rainey, 2000). Cross-sectional area and watershed area are often correlated within a stream network (Leopold et al., 1964), but may not be correlated when compared among streams in watersheds with varying hydrology and geomorphology. For example, the ratio of watershed area to cross-sectional area is higher in desert streams with a greater proportion of subsurface flow than in less variable temperate streams where watershed area is more directly related to surface flow.

For streams, the question being asked – does ecosystem size influence food-chain length – does not provide guidance *a priori* for the appropriate measure of ecosystem size because both measures (resource shed and cross-sectional area) are appropriate for the question. Rather, the appropriate measure of ecosystem size depends on the answer to that question, which poses an interesting circular problem. If resource availability is the determinant of food-chain length, as is specified by the productive-space hypothesis, then watershed area (or some other measure of the resource shed) is the appropriate measure of ecosystem size. If, instead, community assembly processes and species interactions determine food-chain length then cross-sectional area or a similar measure of ecosystem size is likely to be most appropriate. The only way to determine which measure of ecosystem size is appropriate is to measure both the resource shed and cross-sectional area simultaneously when studying food-chain length and let the data determine which measure of ecosystem size best fits the data — and, therefore, which mechanism(s) is regulating food-chain length.

5. Spatial and temporal domains in geomorphology and ecology

Wrapped around the discussion of defining boundaries for ecosystems are general issues of similarities and differences in the spatial and temporal domains of geomorphology and ecology. A full discussion of these issues is not possible in this context, but we can highlight a few issues we find most interesting, focusing for simplicity on aquatic ecosystems only.

5.1. Geomorphic constraints on ecosystem size and food web interactions

Geomorphology has the potential to constrain interactions of the food web at a range of temporal and spatial scales. At long time scales and at the spatial scale of entire landscapes, geomorphology is the ultimate constraint on ecosystem size, regardless of the measure of ecosystem size used. For example, in the Northern Highlands Lake district of Wisconsin, lake area is correlated with the landscape position and is likely a consequence of the geomorphic history (the Wisconsin glaciation) of the region (Riera et al., 2000). The key observation is that lakes low in the landscape are larger and have more complex shapes than lakes high in the landscape (Kratz et al., 1997; Riera et al., 2000). Most lakes in this district were formed when blocks of ice left behind by retreating glaciers melted forming small, typically round, kettle lakes (Hutchinson, 1957; Riera et al., 2000). Larger lakes were likely formed by the coalescence of multiple smaller kettle lakes or where depressions blocked by terminal moraines filled with outwash waters (Riera et al., 2000). Patterns such as these also highlight a potential direct link between geomorphology and the structure of the food web where food-chain length is determined by ecosystem size (Post et al., 2000).

At the channel reach spatial scale and at the modern temporal scale (sensu Schumm and Lichty, 1965), geomorphology can influence the top of the food chain and the bottom. For instance, systematic changes in channel hydraulic geometry and associated velocity (Leopold and Maddock, 1953; Vannote et al., 1980) can constrain the potential spatial range of a predator to particular regions of a watershed because of the dependence the predator has on particular flow or velocities (Hart and Finelli, 1999; Power and Dietrich, 2002) and can mediate predator–prey and competitive interactions (Hart and Finelli, 1999), and channel shape can influence the susceptibility of fish predators to piscivorous birds (Power, 1984; Power et al., 1989), both of which can modify top–down control in stream food webs. Likewise, sediment size or substrate type (e.g., boulders vs. gravel) may have strong effects on interaction strength within stream food webs (Power, 1992; Hart and Finelli, 1999). The presence of deep pools within a stream reach, or inclusion of deep pools in an analysis, often increases food-chain length because it incorporates fish not otherwise found in or considered by typical small scale approaches to stream food web ecology (Finlay et al., 2002). Alternatively, systematic changes in channel morphology (e.g., downstream hydraulic geometry, Leopold and Maddock, 1953) can also drive systematic spatial variability in primary production in streams (Vannote et al., 1980; Stanley et al., 2004), thus, driving a bottom-up control on the aquatic food web. Channel morphology also controls the source and sink nature of stream reaches for organic matter (Bilby and Likens, 1980), invertebrates (Finlay et al., 2002) and fish (Finlay et al., 2002, Schlosser, 1995). In addition, proximity to the ocean and an available stream connection to the ocean are both geomorphologically derived prerequisites for the presence of anadromous fishes. Because spawning mortality of anadromous fishes often depends upon the distance traveled during migration, lakes further from the ocean are likely to be less impacted by anadromous fishes and are, therefore, more likely to be functionally more “well-bounded” than those near the ocean. Whether these systematic trends in watershed geomorphology, and the associated alterations of the food web, are evident over the watershed scale remains for the most part unknown but a potentially fruitful area of coupled ecological and geomorphic research (Power and Dietrich, 2002; Benda et al., 2004).

At the smaller spatial scale of the observed flow characteristics and the present temporal scale (sensu Schumm and Lichty, 1965), geomorphology has only a very local influence on hydraulic characteristics of depth, velocity and turbulence. Even at this fairly small scale, however, Finlay et al. (1999, 2002) found that energy (carbon) sources for stream organisms vary from highly localized (i.e. mm's for invertebrate grazers) to highly diffuse (i.e. potentially km's for detrivorous invertebrate shredders and filter feeders) for organisms that exist within the same habitat in streams. This work makes it clear that geomorphology can strongly regulate carbon flows in streams, but the great diversity in resource use and transport in open systems presents some real challenges for assessing the scale of interactions in streams (Finlay et al., 2002). In contrast, in well-bounded ecosystems like lakes, carbon flow into and through the food web is relatively well constrained, and lake size has a strong and consistent influence on the relative contribution of carbon from littoral and pelagic resources to top predators (Post, 2002; Schindler and Scheuerell, 2002).

5.2. Linkages between darwinian and geomorphological evolution

Darwinian (organismal) and geomorphic evolution may be linked in a variety of ecosystems at multiple temporal scales. Examples include the role of geomorphology in mediating hydrologic variability and, subsequently, the evolution of life history among many aquatic organisms (e.g., Lytle, 2002; Lytle and Poff, 2004). Geomorphic changes at regional and catchment scales can isolate populations and allow for sympatric speciation and rapid evolution (Stearns, 1983; Losos, 1994; Reznick et al., 1996; Hairston et al., 1999; Losos and Schluter, 2000; Montgomery, 2000; Reznick et al., 2001). For example, the tectonic forces that created the geologically young mountain ranges along Pacific Rim, and the resulting long-term geomorphic evolution of habitat in stream channels, may help explain differences in rates of speciation between Pacific and Atlantic salmon (Montgomery, 2000).

5.3. Human alterations of geomorphology

In addition to systematic geomorphic variations described above, over modern timescales human activities can have profound impacts upon the geomorphology and ecology of ecosystems. For example, the construction of dams fundamentally alters the distribution of fish, invertebrates, and other aquatic organisms, and also modifies the geomorphology and flow regime of streams upstream and downstream of the dam (Ligon et al., 1995). These abiotic changes alone impact local food web processes, although the cumulative impacts of dams on the structure of the food web of the entire watershed remains unknown. In addition to dams, floodplain geomorphology and hydrology has been shown to have profound impacts on all levels of floodplain food webs (Power et al., 1995a, b), and, thus, the construction of levees can also drive large scale changes in the structure of the food webs via geomorphic alterations. Likewise, because of the proximity to the coast and human populations, many estuaries have been fragmented by human activities such as building tide gates, roads or railroads (Anisfeld and Benoit, 1997; Portnoy and Giblin, 1997; Anisfeld et al., 1999; Portnoy, 1999). The resulting constriction of tidal exchange alters rates of sedimentation and biogeochemical cycling (Roman et al., 2000; Roman et al., 2002), reduces habitat quality for many estuarine fish species (Layman et al., 2004), and limits biological linkages between estuaries and the coastal ocean (Roman et al., 2002; Raposa and Roman, 2003; Layman et al., 2004, 2005). In estuaries in the Bahamas, hydrologic fragmentation has substantial impacts upon fish community structure and food web structure (Layman et al., 2004, 2005). In all, human modification of geomorphology has important implications for the structure of the food web and ecosystem processes, and that we are only recently beginning to understand some of these linked impacts (Power et al., 1995b; Power et al., 1996a; Doyle et al., 2002; Stanley and Doyle, 2002; Doyle et al., 2003a; Doyle et al., 2003b).

6. Conclusions

A common conceptualization of ecosystems is crucial for forging stronger linkages between geomorphology and ecosystem ecology. Because ecosystem processes are scale dependent, the choice of boundaries is of profound importance to our common view of an ecosystem and to the scope and validity of questions being asked within that ecosystem. Ecosystems have been defined in numerous ways. Different definitions derive, in part, from different traditions in ecology and geomorphology, but we note that the over-reliance upon physical or structural definition of boundaries can obscure boundaries related to important ecological processes and interactions. Ecosystems in which a strong congruence occurs among physical boundaries, community interactions, and ecosystem processes can be considered well-bounded. In well-bounded ecosystem, one or a few different definitions of an ecosystem may be sufficient for most questions. In contrast, in open ecosystems where there is little or no congruence among physical and functional boundaries, there are many functionally appropriate definitions of an ecosystem and many possible ways to delineate ecosystem boundaries. In these systems, each different question may dictate very different definitions of ecosystem boundaries. Furthermore, for questions that bridge the population–community and process–function approaches of ecology, such as many questions in food web ecology, the appropriate measure of ecosystem boundaries may not depend on the question being asked but rather on the answer to that question. In general, geomorphology and ecology interact strongly at short and long temporal scales. Advances in linking ecology and geomorphology will likely emerge more powerfully by simultaneously and explicitly considering the temporal and spatial scale of variation in both geomorphic and ecological systems.

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