

IDEA AND PERSPECTIVE

Historical foundations and future directions in macrosystems ecology

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Abstract

Macrosystems ecology is an effort to understand ecological processes and interactions at the broadest spatial scales and has potential to help solve globally important social and ecological challenges. It is important to understand the intellectual legacies underpinning macrosystems ecology: How the subdiscipline fits within, builds upon, differs from and extends previous theories. We trace the rise of macrosystems ecology with respect to preceding theories and present a new hypothesis that integrates the multiple components of macrosystems theory. The *spatio-temporal anthropogenic rescaling (STAR) hypothesis* suggests that human activities are altering the scales of ecological processes, resulting in interactions at novel space–time scale combinations that are diverse and predictable. We articulate four predictions about how human actions are “expanding”, “shrinking”, “speeding up” and “slowing down” ecological processes and interactions, and thereby generating new scaling relationships for ecological patterns and processes. We provide examples of these rescaling processes and describe ecological consequences across terrestrial, freshwater and marine ecosystems. Rescaling depends in part on characteristics including connectivity, stability and heterogeneity. Our STAR hypothesis challenges traditional assumptions about how the spatial and temporal scales of processes and interactions operate in different types of ecosystems and provides a lens through which to understand macrosystem-scale environmental change.

Keywords

Hierarchy theory, landscape ecology, macrosystems ecology, space–time, spatio-temporal.

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INTRODUCTION

Macrosystems ecology is an emerging subdiscipline that emphasises the study of ecological phenomena at regional to continental spatial scales (Heffernan *et al.* 2014), typically conducted at scales of 100s to 1000s of km². A principle motivation for the study of macrosystems is the growing awareness of the prevailing influence of human activities on ecosystem dynamics globally (Ellis 2015). The sheer magnitude of human impacts makes it nearly impossible to understand cause and predict effect at these broader spatial scales using observations and experiments conducted at only local or regional scales. Given the many ways human activities are disrupting ecological interactions across spatio-temporal scales, macrosystems ecology thus presents an opportunity to understand regional-to-continental scale pattern and process as well as novel scaling laws governing ecological interactions.

Macrosystems ecology draws on interacting hierarchical networks of biological, geophysical and societal components (Heffernan *et al.* 2014). Hierarchical interactions can produce different patterns depending on the nature of interaction. As a means to understand macrosystem-scale patterns, macroscale

phenomena have so far been organised into four categories: macroscale feedbacks, cross-scale emergences, cross-scale interactions and teleconnections (Heffernan *et al.* 2014; Soranno *et al.* 2014). When multiple broad-scale variables interact, such as between precipitation and vegetation types (e.g. Keys *et al.* 2016), macroscale feedbacks occur. When fine-scale processes operate synchronously to impact broad-scale patterns, cross-scale emergences occur (e.g. synchronous winter application of road salt in many watersheds increases freshwater salinity regionally, Kaushal *et al.* 2005). When a variable influences how a broad-scale process influences a fine-scale process, a cross-scale interaction occurs (e.g. lake water clarity influences the sensitivity of lake temperatures to climate change, Rose *et al.* 2016). Finally, when a fine-scale variable at one location influences a fine-scale variable at a geographically distant location, a teleconnection occurs (e.g. variations in the East Pacific teleconnection and Pacific Decadal Oscillation influence area burned in boreal Alaska, USA; Duffy *et al.* 2005).

Macrosystems ecology developed from a rich intellectual legacy of ecological theory spanning many decades. To be most effective at providing new insights, it is important to

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understand this intellectual legacy, how this emerging subdiscipline fits in with, builds upon and extends previous theories, as well as the key features that make macrosystems ecology distinctive. Similar to landscape ecology (Turner & Gardner 2015), macrosystems ecology explicitly considers scale and heterogeneity and emphasises relationships among biological, geophysical and sociocultural components, but macrosystems ecology extends to even larger spatial extents (Heffernan *et al.* 2014). Here, we trace the rise of theory of how processes and interactions scale across time and space, the importance of interactions and heterogeneity and the increasing importance of coupled social-ecological systems research in macroscale frameworks that are precursors to macrosystems ecology. From this perspective, we take the essential elements that emerge from the intellectual foundations of macrosystems ecology to develop a new hypothesis about how anthropogenic activities are rescaling ecological processes in space and time. Based on this hypothesis, we then develop testable predictions to understand macroscale phenomena. Finally, we summarise some of the challenges and frontiers for the emerging subdiscipline of macrosystems ecology in the context of the proposed hypothesis.

HISTORICAL FOUNDATIONS OF MACROSYSTEMS ECOLOGY

These ecosystems as we call them... form one category of the multitudinous physical systems of the universe, which range from the universe as a whole down to the atom. The whole method of science... is to isolate systems mentally for the purposes of study... Actually the systems we isolate mentally are not only included as parts of larger ones, but they also overlap, interlock, and interact with one another. Tansley 1935, 299–300

That there is no single correct scale or level at which to describe a system does not mean that all scales serve equally well or that there are not scaling laws. Levin 1992

Macrosystems ecology did not arise *de novo*, but rather draws from a legacy of conceptual theories on scale, hierarchy, landscape ecology and social-ecological systems. We briefly highlight these historical intellectual roots of macrosystems ecology, emphasising key conceptual and empirical advances that have helped shape theory and perspective. The richness of thought in these foundational preceding studies is very deep. We suggest that macrosystems ecology blends and builds on these roots and that advancements in measurement capacity and data availability may now allow conceptual frameworks proposed decades ago to be tested empirically across very large spatial extents.

Ecologists recognised long ago that patterns and processes change over space and time, and that spatial and temporal scales of natural processes are often positively correlated. The oceanographer Henry Stommel created the classic “Stommel diagram” to illustrate variation in ocean characteristics such as sea level across temporal and spatial scales (Stommel 1963). This diagram was modified and first applied to

ecological relationships by Haury *et al.* (1978) to show how tightly linked processes at different scales, from micropatches to ice age variations, influenced plankton productivity. In terrestrial ecology, a similar diagram was developed by Delcourt *et al.* (1983; Fig. 1) to depict space–time linkages for disturbance regimes, biotic responses and vegetation patterns. Within their diagram, Delcourt *et al.* (1983) integrated the large, slow processes (e.g. glacial–interglacial cycles, speciation, species migration) studied in palaeoecology with the local, fast processes (e.g. disturbance, succession and species interactions) emphasised in community and ecosystem ecology. These space–time frameworks offered a structured way to consider ecological processes over a wide range of scales and have been applied widely in ecology, but they dealt little with processes that interacted across scales, the possibility of rules governing how processes and relationships might scale or how anthropogenic processes influenced these scaling relationships.

Biogeography theory, which emphasises understanding broad-scale spatial patterns in species distributions and community assemblages, has been an important component of ecological research since at least the time of Darwin and Wallace (Nelson 1978; Brown 2001). Elements of biogeography theory were codified more recently in concepts such as island biogeography (MacArthur and Wilson 1967), which posited that the number of species scales with area, and species richness is determined by the opposing forces of immigration and extinction. Recognition of the ecological importance of scale grew during the 1980s, as integration of concepts from general systems theory (von Bertalanffy 1968) and ecological scale led to the emergence of hierarchy theory to understand ecological consequences of organisational levels, from cells to organisms, communities, ecosystems and the biosphere (Allen & Starr 1982; O'Neill *et al.* 1986).

Hierarchy theory posits that in a set of interconnected components (a hierarchy) the higher-level components constrain lower-level components and lower levels can interact to influence higher-level outcomes. In hierarchy theory, the concept of scale refers to the spatial or temporal dimensions of one of these components, whereas the level of organisation identifies the component's position within an ecological hierarchy (Allen & Starr 1982). As a result, hierarchy theory also emphasises the need to consider multiple levels of organisation in any study (O'Neill *et al.* 1986): a focal level based on the question or objective of the study, as well as the levels above and below the focal level (Fig. 2). The level above the focal level constrains and controls the lower levels, providing context. The level below the focal level includes the details needed to explain behaviour observed at the focal level, providing mechanism. For a given focal system, boundaries of possible operating space are jointly formed by interacting components at lower and higher organisational levels, forming a constraint envelope across time and space, which is analogous to a niche hypervolume (O'Neill *et al.* 1986). As recognised in the earlier space–time diagrams, system process rates are generally slow at broad spatial extents and fast at fine spatial extents. Thus, no single scale is appropriate for all studies, and scales of analysis must match the space–time scales of the focal object or process; mismatched scales can lead to erroneous inference

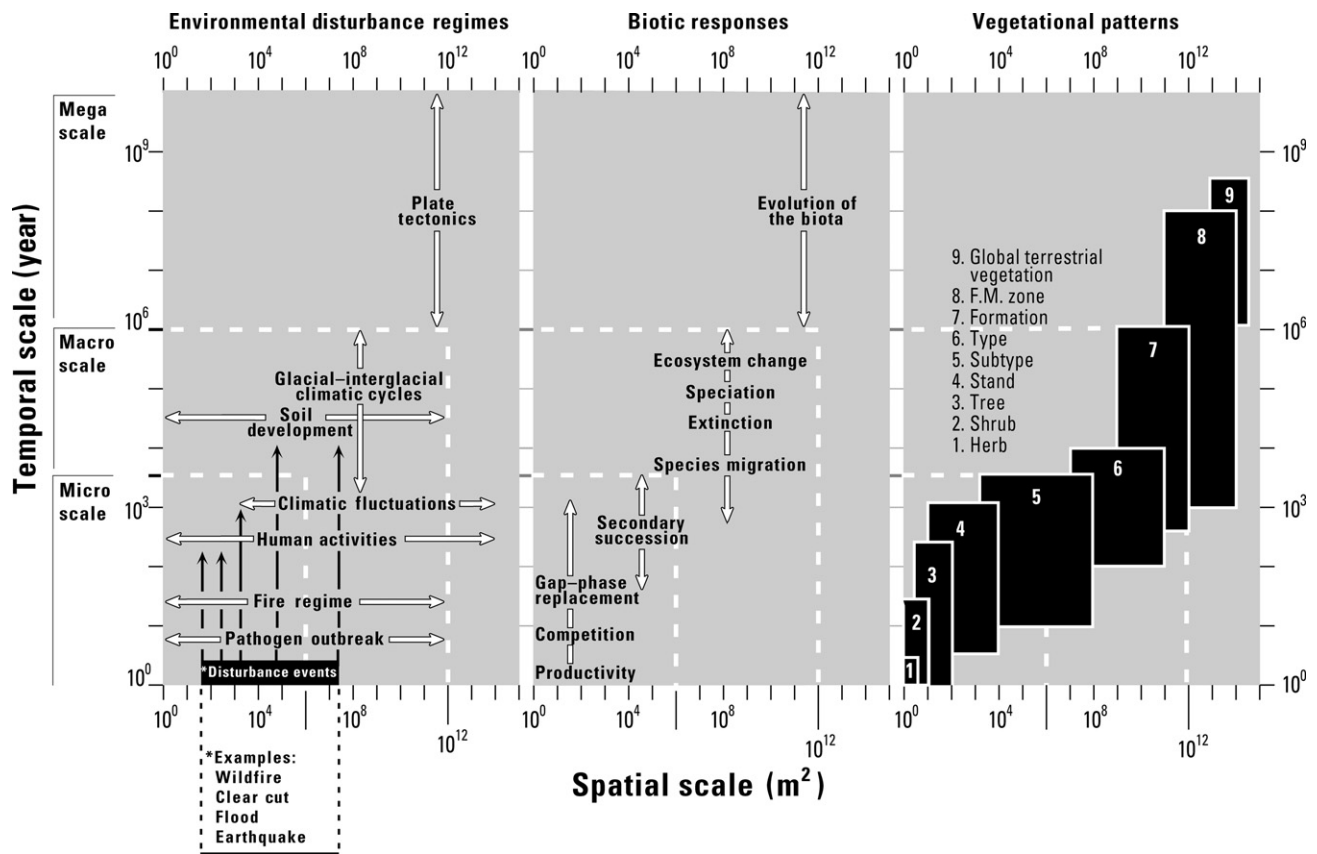


Figure 1 Correlations between the spatial and temporal scales of ecological processes have long been recognised in both aquatic and terrestrial ecosystems, as first proposed by Stommel (1963), presented by Delcourt *et al.* (1983) and reprinted with permission from Turner & Gardner (2015).

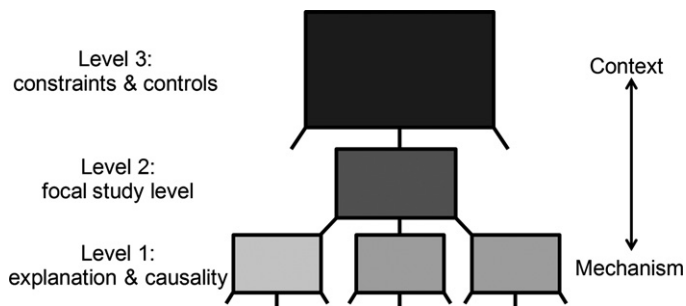


Figure 2 Hierarchy theory emphasises the need to study at least three levels of organisation, but there is no single correct or appropriate level at which a study system can be described. Adapted from O'Neill *et al.* (1986).

(Allen & Starr 1982). Interactions among components are strongest when they operate at the same scales, but processes from different scales may interact in ways that amplify or dampen the amplitude and rate of system dynamics (Peters *et al.* 2004). This can produce macroscale feedbacks, cross-scale emergences, or cross-scale interactions (Heffernan *et al.* 2014; Soranno *et al.* 2014). Because processes are contingent upon system dynamics at lower and higher levels of organisation, perturbations to one level can cascade across scales with unanticipated and potentially large consequences. Thus, understanding scaling rules is imperative to understanding potential nonlinearity in interactions and feedbacks.

Concurrent with development of scale concepts, studies of large, spatially heterogeneous areas grew in the 1980s with the emergence of landscape ecology (Urban *et al.* 1987; Turner 1989, 2005). Landscape ecology focuses on the relationships between spatial pattern and ecological processes, including the causes and consequences of spatial heterogeneity across a range of scales, and recognises “landscape” as a hierarchical level (Urban *et al.* 1987). Landscape ecology combined approaches from geography with functional approaches of ecology and often focused on spatial extents much larger than those traditionally studied in most other subfields of ecology (Turner & Gardner 2015). While landscape ecology is applied across a range of scales, it typically does not extend to continental extents. In contrast, macrosystems ecology strongly emphasises the broadest of spatial extents. This emphasis is urgently needed because so many anthropogenic activities are impacting the planet at very broad spatial scales. In addition, although landscape ecology directly addresses lateral fluxes of organisms, matter and energy, concepts such as teleconnections that deal with geographically remote relationships are a component of macrosystems ecology but not commonly addressed in landscape ecology. The advent of macrosystems ecology enables new lines of research to understand impacts of anthropogenic processes at large spatial extents.

Explicit treatment of spatial heterogeneity and a focus on broad spatial scales have been facilitated by technological advances (e.g. remote-sensing and geographic information

systems), which, now coupled with high-frequency sensing technologies, modern cyber-infrastructure and data repositories, have also helped set the stage for macrosystems ecology. Landscape ecology offered concepts, methods and models for incorporating space and for extrapolating across scales (Miller *et al.* 2004). When integrated with concepts from hierarchy theory, landscape ecology also contributed to development of cross-scale interactions and nonlinear dynamics (Peters *et al.* 2004), both of which are of important elements in macrosystems ecology.

Macrosystems ecology explicitly recognises humans as an important interacting system component in hierarchical systems, thus building on a substantial body of work investigating social-ecological systems (Binder *et al.* 2013; Heffernan *et al.* 2014). The coupling of human and natural systems in ecological research emerged from two major conceptual shifts: seeing ecosystems as dynamic, non-equilibrium systems and understanding that anthropogenic activities are integral components of all ecosystems (Folke 2006). In the early 20th century, ecological research sought to understand ecosystem successional development. Whether ecosystems were seen as ontogenic units or as composed of multiple interacting components, ecological change was largely perceived as a predictable, stable process that was influenced by exogenous factors like disturbance (Tansley 1904; Connell 1978). In the latter half of the 20th century, theoretical research began to question how stable and predictable systems were when faced with disturbance (May 1973). This work sparked current understanding of ecosystems as non-equilibrium systems that can exhibit strong nonlinearity in their development and response to disturbance.

Frequently in early ecological studies, human activity was seen as an occasional exogenous factor that disrupted ecological processes, but not viewed as integral to ecosystem operation or essential for defining the characteristics of an ecosystem. In this manner, while anthropogenic activity could influence a system, important feedbacks and equilibria were viewed as internal to the natural system rather than occurring between social and ecological systems.

Beginning in the 1990s, this framework shifted as ecologists and social scientists increasingly recognised that human influences were ecologically important and globally pervasive (Vitousek *et al.* 1997; Westley *et al.* 2016; Hobbs *et al.* 2014). Human activities, in concert with other external drivers, could lead to rescaling of landscape processes, press-pulse disturbance dynamics, broad-scale feedbacks and cross-scale effects in social-ecological systems (Urban *et al.* 1987; Walker *et al.* 2004; Liu *et al.* 2007a; Collins *et al.* 2010). As recognition of complex feedbacks between social and ecological systems grew, humans were incorporated as an integral, endogenous component of system operation (Collins *et al.* 2010). Ecology was neither a subcomponent of social systems nor was society a subcomponent of ecological systems; rather, social-ecological systems were a system unto themselves, encompassing concepts such as resilience and sustainability (Walker *et al.* 2004; Liu *et al.* 2007a; Folke *et al.* 2008) and subject to globalising forces (Young *et al.* 2006). The social-ecological systems framework led to better integration of social science and natural science research, which has enabled greater understanding

of feedbacks between the two component systems and the cross-scale, nested and telecoupled effects of these interactions (e.g. Adger *et al.* 2009), themes that persist in macrosystems ecology.

Efforts to understand broad-scale relationships between organisms and their environments, termed macroecology, emerged at about the same time as social-ecological systems research (Brown & Maurer 1989). Generally, limited to understanding broad-scale spatial patterns among and within species rather than representing all ecological entities, macroecology cuts across the above-mentioned foundational theories and emphasises synoptic assessments of patterns such as latitudinal variations in organisms, allometric scaling rules, species richness and other biodiversity characteristics (Holling 1992; Brown 1995; Gaston & Blackburn 2007). This organism-centric approach precludes it from addressing many interacting hierarchical processes regulating ecological change.

Beginning with the earliest studies of ecological succession, ecologists have often employed space-for-time substitutions and long-term studies to understand broad-scale ecosystem pattern and process (Pickett 1989). However, the substantial ecological variability inherent to the macrosystems scale, as well as the disrupting nature of human activities to traditional ecological space-time interactions, necessitates an integrated approach that leverages historical foundational frameworks as well as contemporary tools and techniques. Today, macrosystems ecology incorporates strands of the diverse array of above-mentioned theories in a multifaceted framework that enables understanding and prediction of broad spatial-scale processes, interactions and scaling laws (Heffernan *et al.* 2014; Gholz & Blood 2016). Macrosystems ecology also benefits from contemporary scientific tools and techniques that have emerged as the advent of preceding frameworks to answer ecological questions at scales previously not tractable (e.g. Wulder *et al.* 2012; Peters *et al.* 2014; Fei *et al.* 2016). The maturation of macrosystems ecology requires development of testable hypotheses and a demonstrated ability to enhance understanding and prediction of ecological process at very broad spatial and temporal scales.

A NEW HYPOTHESIS FOR UNDERSTANDING HUMAN IMPACTS ON ECOLOGICAL SYSTEMS

We present a new hypothesis, the *spatio-temporal anthropogenic rescaling (STAR) hypothesis*, that builds on the intellectual legacy of conceptual theories that inform macrosystems ecology. We integrate preceding theories in a macrosystems framework and describe social-ecological system feedbacks across space and time to posit that, at the large spatial extents characterising macrosystems ecology, anthropogenic drivers are rescaling spatio-temporal ecological interactions. Based on this hypothesis, we articulate four predictions about how human actions are “*expanding*”, “*shrinking*”, “*speeding up*” and “*slowing down*” ecological interactions, and thereby generating new scaling rules governing ecological pattern and process. We provide examples of these rescaling processes, describe some of the associated ecological consequences and quantify the scale and impact of these changes (Table 1). Such changes, which we argue are

Table 1 The spatio-temporal anthropogenic rescaling (STAR) hypothesis contains four predictions about how human activities are “expanding”, “shrinking”, “speeding up” or “slowing down” ecological interactions and processes. The examples provided are summarised for each prediction category

STAR impact	Prediction	Examples
Expansion	Rapid and frequent processes that normally occur over confined spatial extent will expand to operate across broader spatial scales	1. Land-use effects on wind erosion 2. Atmospheric N deposition on northern-hemisphere lakes 3. Grazing and fire-suppression effects on shrub encroachment
Shrinking	Processes that might naturally operate over broad spatial extents (at longer temporal scales) will be spatially condensed and confined	1. Channelling rivers 2. Shrinking animal migration corridors
Speeding up	The rate of many broad-scale processes will increase, shortening the temporal over which the process occurs	1. Accelerating rates of climate warming 2. Facilitating frequent, long-distance species dispersal
Slowing down	Processes will slow down such that they are unusually persistent over a given spatial extent	1. Land-use legacies effects on biogeochemical processes

inherent to social-ecological systems, could push these systems to deviate from the spatio-temporal operating space traditionally associated with natural systems and therefore have important implications for ecosystems, the organisms that inhabit them and how they are managed (Fig. 3). These changes may challenge traditional assumptions about how the spatial and temporal scales of processes and interactions operate (Fig. 1).

Using empirical studies, we describe how, due to human impacts, processes that historically operated at short time scales and localised spatial extents are now operating across unusually broad spatial extents (expansion), and many processes that historically operated at broad spatial extents are being constrained to fine spatial extents (shrinking). Similarly, processes that historically operated over long time scales and broad spatial extents are becoming unusually fast over large areas (speeding up), and many processes that historically operated at short time scales are increasingly persistent through time (slowing down). While we recognise that human activity can alter both spatial and temporal scales of ecological processes simultaneously, for simplicity, we focus on substantial shifts in only one scale (time or space) at a time.

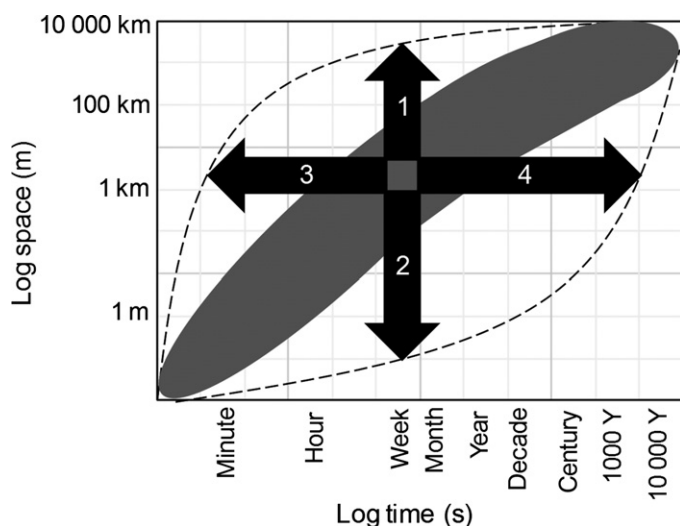


Figure 3 The spatio-temporal anthropogenic rescaling hypothesis posits that human activities are rescaling ecological phenomena through (1) expansion, (2) shrinking, (3) speeding up and (4) slowing down processes and interactions such that historical relationships (gray) are now operating within a much larger spatio-temporal envelope (dashed lines).

Expansion

Anthropogenic drivers are rescaling ecological processes and interactions such that rapid processes that normally occur at local scales are “expanded” to operate across much larger spatial extent. Large dust storms offer a classic example for this rescaling (Kellogg & Griffin 2006; Field *et al.* 2010). Wind erosion can sometimes occur at a local spatial extent for a short time span, especially when it is driven by microscale wind speed and atmospheric humidity (Toy *et al.* 2002). Human-induced land-use changes and land degradation (e.g. intensive agriculture and livestock grazing), however, can reduce vegetation cover at broad scales and increase spatial connectivity of unvegetated gaps. These changes ultimately alter land–atmosphere feedbacks, causing fine-scale wind erosion to propagate nonlinearly to sometimes produce massive continental dust storms (Cook *et al.* 2009) which can have global implications (Jickells *et al.* 2005). Historically, catastrophic widespread dust storms have been documented in many regions, including the US Great Plains (Worster 1979), Sahara-Sahel region of Africa (Kellogg & Griffin 2006), semi-arid region of China (Liu *et al.* 2007b) and northeastern Australia (Ludwig *et al.* 2007). “Expansion” fits within the macrosystems ecology category of “cross-scale emergence”, as the effects of changes that occur at fine spatial scales accumulate, thereby propagating across much larger spatial extents (Heffernan *et al.* 2014).

In aquatic systems, another example of how human activities are expanding the spatial extent of ecological processes is the observation of widespread anthropogenically driven N deposition in lakes and oceans (Holtgrieve *et al.* 2011; Kim *et al.* 2011). Historically, N inputs to aquatic ecosystems were driven primarily by local point and non-point sources. But evidence shows that anthropogenic CO₂ emissions, fossil fuel consumption and widespread industrial N production and uses are expanding the spatial footprint of this otherwise local process of N inputs (Galloway *et al.* 2008; Elser *et al.* 2009). For example, N emissions from urban areas rapidly spread across large spatial extents (Fenn *et al.* 2003). Thus, regional-to-continental scale N inputs are increasing algal biomass in many regions, altering ecological stoichiometry and food-web interactions at time scales not observed historically (Saros *et al.* 2003; Elser *et al.* 2009; Holtgrieve *et al.* 2011).

Expansion also encompasses other situations in which anthropogenic activities enable local processes to become ubiquitous and thereby occur across very large spatial extents. For example, in arid or semi-arid regions, woody plant encroachment into grassland is rapidly occurring in many regions worldwide (Archer *et al.* 1988; Roques *et al.* 2001; Briggs *et al.* 2005). Competition and dispersal are the fine-scale processes that normally control for shrub colonisation and grassland loss (Fowler 1986). However, in many regions anthropogenic disturbances such as livestock grazing and altered fire regimes can suppress grass and favoured shrub colonisation over large areas (Archer *et al.* 1995). When grass cover is reduced to a certain extent, land–atmosphere interactions can be altered so that broad-scale processes (e.g. increased aridity) become the dominant factors driving vegetation change and desertification (Archer *et al.* 1995; Peters *et al.* 2007).

Shrinking

Some anthropogenic impacts are shrinking the spatial scale of ecological processes and interactions, such that processes and interactions that might naturally operate over broad spatial extent (at longer temporal scales) have been spatially condensed and confined by anthropogenic changes. This phenomenon often means that the effects of the constrained ecological process are more severe but localised, leading to larger impacts per unit area. An example of shrinking is the disconnection of fluvial systems from their floodplains through anthropogenic channellisation of rivers. In many cases, severe floods occur infrequently yet can be ecologically important in providing spatial linkages between rivers and adjacent floodplains (Poff *et al.* 1997; McCluney *et al.* 2014). In this case, the disconnection from rivers and their associated riparian flood plains concentrates the river flow, thereby leading to greater erosion and a number of associated detrimental ecological impacts on the river ecosystems (Brooker 1985; Gregory 2006). For example, changes in the physical structure of river channels consistently lead to changes in the biotic community composition, usually with a reduction in river biodiversity (Sedell *et al.* 1990; Boon 1992) and increased frequency of upland species in floodplain forests (Gergel *et al.* 2002). Human activities are also shrinking a number of marine ecosystem features. For example, shrinking Arctic sea ice is a primary driver of increasing primary production in the Arctic (Arrigo *et al.* 2008). In addition, overfishing has led to the collapse of many marine fish taxa, thereby shrinking the range of many species (Kramer & Chapman 1999).

Similar to how human activities have constrained river–floodplain connections, human activities have shrunk the size of animal migration corridors, thereby focusing and magnifying the impact of migrations as animals move through smaller spaces than would otherwise occur without changes in land use/land cover. For example, increased channelling of grazers, such as deer and elephants, through spatially constricted wildlife corridors leads to a greater intensity of grazing (Tedonkeng Pamo & Tchamba 2001; Reimers *et al.* 2007), which can in turn modify system-level vegetation dynamics (Tedonkeng Pamo & Tchamba 2001; Croomsigt & Olf 2008). While the

per capita impact of migrating animals increases, reduced corridor space constrains genetic exchange due to restricted dispersal (Bartzke *et al.* 2015; Skarin *et al.* 2015). This leads to a shrinking in the scale of the exchange of genetic information to isolated pockets of populations and can facilitate high levels of inbreeding (Holderegger & Di Giulio 2010; Titus *et al.* 2014), which can change local patterns of biodiversity and population viability.

Speeding up

In contrast with anthropogenic impacts that lengthen the temporal scale over which a process occurs, human activity has also accelerated the rate of many broad-scale processes, thereby shortening the temporal scale over which the process occurs. Examples of such rescaling include many global issues such as climate change, broad-scale species dispersal and colonisation and broad-scale shifts in land use.

Rapid increases in greenhouse gas concentrations due to industrialisation have resulted in unprecedented and accelerating rates of global warming (Cox *et al.* 2000; Stocker *et al.* 2013), increasing frequency of extreme events and unusually high rates of sea-level rise in comparison to the last two millennia (Church *et al.* 2013; Cai *et al.* 2014). Recent global warming rates of ~ 0.2 °C per decade, combined with global climate models projections of 1.5–6 °C of warming under high carbon dioxide scenarios in the 21st century, suggest that anthropogenic climate change will lead to increasingly rapid warming as compared to palaeoclimate records (Hansen *et al.* 2006; Stocker *et al.* 2013). Rapid climate change has resulted in macroscale feedbacks between regional climate and vegetation patterns (Heffernan *et al.* 2014) and marine ecosystems (Niiranen *et al.* 2013) that are expected to generate global, continental and regional impacts throughout natural and human systems. The rates of change in these global processes and characteristics represent critically important examples of speeding up.

Human-assisted species dispersal has increased the rate and changed the patterns of colonisation and invasion throughout the globe by vaulting over natural biogeographic barriers (Ricciardi 2007). Long-distance trade and increased human travel have resulted in the intentional introduction of some species and accidental introduction of “hitchhiker” species in terrestrial and aquatic systems worldwide (Lodge *et al.* 2006; Hulme 2009). In aquatic systems, invasive species are well known to restructure terrestrial, freshwater and marine food webs and can lead to substantial economic impacts (Pimentel *et al.* 2005; Vilà *et al.* 2010). Long-distance dispersal of organisms can occur through natural forces, such as wind and ocean currents, but studies tracking origins of non-native species suggest that these movements are insignificant as compared to human-assisted dispersal (Mack & Lonsdale 2001). For example, a study of non-native invertebrate plant pests in Great Britain found that human-assisted introductions are double the rate of natural colonisation (Smith *et al.* 2007). Similarly, rapid long-distance transport and contemporary harvesting techniques can facilitate the “contagious resource exploitation” of economically important species, hastening regional-to-global declines in some species (Eriksson *et al.* 2015).

Globalisation and telecoupling – environmental and socio-economic interactions among coupled systems over long distances – have led to broad scale and rapid changes in land use (Liu *et al.* 2013). Soybean trade increased rapidly during the first part of the 21st century between South America and Asia and Europe (Garrett *et al.* 2013; Food and Agriculture Organization of the United Nations Statistics Division 2016). In response, soybean production area expanded by more than 30 million hectares between 1986 and 2010 in South America, resulting in conversion of tropical savannah and tropical forests (Brannstrom *et al.* 2008; Macedo *et al.* 2012). Rapid and broad-scale shifts in land use in the tropics could result in “macroscale feedbacks” (Heffernan *et al.* 2014) to the climate system, further highlighting the need to understand how human activity may rescale these interactions in macrosystems ecology research.

Slowing down

In general, anthropogenic activities are increasing ecological rates of change (Vitousek *et al.* 1997). However, some anthropogenic activities are rescaling ecological interactions and processes temporally by slowing them down such that the effects of short-term events can be unusually persistent over a given spatial extent. An example of this type of temporal shift is the concept of land-use legacies – the enduring consequences of past human impacts on ecosystem structure and function (Foster *et al.* 2003; Perring *et al.* 2015) – whereby human influence on patterns or processes is detectable for decades or even centuries after the causal disturbance has ended and natural processes have reestablished. Land-use legacies are ubiquitous today, affecting a variety of ecosystem characteristics across both aquatic (Christensen *et al.* 1996; Harding *et al.* 1998) and terrestrial (Dupouey *et al.* 2002; McLauchlan 2006) ecosystems. The types of anthropogenic drivers involved are similarly diverse, ranging from agriculture and logging to the modification of disturbance regimes (Foster *et al.* 2003).

Often, legacies occur when fast-operating processes (e.g. human disturbances) interact with slowly changing characteristics or processes (e.g. species extinctions or habitat structure). The magnitude of perturbation and the sensitivity or recovery rate of the affected ecological characteristic determine how long a legacy continues to have effects. In freshwater systems, legacies of human land use can influence aquatic biodiversity for decades. In western North Carolina streams, Harding *et al.* (1998) found that present day diversity of fish and invertebrates was best predicted by whole-watershed land-use five decades previous, with agricultural legacies continuing to limit stream diversity despite widespread reforestation. This lack of recovery can be explained in part by habitat modification. Clear cutting, a consequence of both logging and agriculture, reduces inputs of large woody debris into stream ecosystems, important for diversifying habitat structure, as well as controlling flow patterns and nutrient release. The effects of this reduced debris can last for decades (Bilby & Likens 1980; Bilby 1981), compounded by the slow recovery times of many macroinvertebrates (Foster *et al.* 2003). Analogous processes occur in lakes. In Wisconsin's North

Temperate Lakes region, for example, development-induced reduction in woody inputs is expected to influence ecosystem processes and structure for up to two centuries (Christensen *et al.* 1996; Marburg *et al.* 2006). These effects can trickle up food webs. For example, macroinvertebrate decline and suppression of fish recruitment due to reduced woody inputs not only impact these populations directly but also the entire food webs (Roth *et al.* 2007).

The same anthropogenic drivers that have influenced the temporal dynamics of aquatic systems exert lasting effects on terrestrial systems as well. Changes in European agricultural land use have led to a substantial decline in natural habitats and consequently time-delayed species extinctions that operate over many decades (Krauss *et al.* 2010). Similarly, land use by Euro-American settlers continues to influence forest composition and structure in the upper Midwestern USA centuries after land conversion and logging ceased (Rhemtulla *et al.* 2009), and forest biodiversity in France has been attributed to former Roman agriculture (Dambrine *et al.* 2007). These structural changes can impact entire food webs for decades, for example, by reducing the abundance of organisms reliant on old growth forest habitat, such as various salamander (Hicks & Pearson 2003) and cavity-nesting bird (Hansen *et al.* 1991) species, both of which play important ecological roles in the forest ecosystem (Bednarz *et al.* 2004; Davic & Welsh 2004). Agriculture is able to exert such a long-lasting influence not only due to deforestation but also through its effects on soil (McLauchlan 2006). Agriculture-driven differences in soil pH, carbon and nitrogen can last for decades to centuries after reestablishment of native species (Fraterrigo *et al.* 2005). Soil-based legacies have been documented not only in forests (Dupouey *et al.* 2002) but also prairies (Matamala *et al.* 2008) and grasslands (Baer *et al.* 2002). Even in highly anthropogenic socioecological systems such as cities, historical land cover can explain many ecological functions and services better than contemporary land-cover patterns (Dallimer *et al.* 2015).

Summary of the STAR hypothesis

Our STAR hypothesis posits that human activities are expanding the scaling envelope of ecological interactions to include novel space–time scale combinations. The rapid growth and reach of anthropogenic processes as well as the frequency of nonlinear ecological processes and interactions are increasing the risks of rapid and permanent ecological regime shifts (Scheffer *et al.* 2001; Rocha *et al.* 2015). This means that traditional assumptions about how the spatial and temporal scales of processes and interactions operate (Fig. 1) must be carefully reconsidered. For example, climate change, which historically occurred slowly over continental scales, is now occurring relatively rapidly, thereby “speeding up”, with substantial negative impacts on services provided by terrestrial, freshwater and marine ecosystems (Rocha *et al.* 2015). This change implies that knowledge of pattern and process at large spatial scales must account for interactions occurring at shorter as well as longer temporal scales because relationships across time and space have been rescaled. Indeed, the many space–time combinations that result from anthropogenic

perturbations produce departures from the traditional space–time relationship (Fig. 3) that challenge scientists to uncover new scaling laws for macroscale ecological phenomena. These challenges highlight the need for robust macrosystems ecology research.

The processes of expanding and shrinking, and of slowing down and speeding up, operate in opposing directions along axes of spatial and temporal scale, respectively (Fig. 3). What characteristics dictate when human activities are likely to “expand” versus “shrink” or “speed up” versus “slow down”? An exploration of some key examples suggests that the rescaling direction depends at least in part on the nature of the human activity and the ecological or biological compartment on which the activity operates. The examples provided herein show that processes that operate predominantly via the atmosphere (e.g. nitrogen deposition, climate change) result in ecological interactions that are expanded or sped up. Processes that operate in the oceans may respond similarly to those in the atmosphere because of the inherent high connectivity and fluidity of the marine environment (Cowen *et al.* 2000). Meanwhile, processes that operate on the landscape seem more likely to produce interactions that slow down and or shrink (e.g. animal migration pathways). However, some animal dispersal pathways or migrations are being constrained (e.g. large animal migrations) while others are being sped up (e.g. many invasive species), highlighting the importance of characteristics of the biotic community and their interactions with human activities.

We hypothesise that the impacts of human activities on spatio-temporal scales of ecological interactions occur differently on the landscape and the atmosphere due to the importance of connectivity. When occurring via highly connected pathways, such as those the atmosphere can provide, anthropogenic changes can rapidly disperse widely across large spatial extents. In contrast, changes on the landscape (e.g. land-use land-cover changes) propagate spatially more slowly. Furthermore, spatial heterogeneity on the landscape may play a key role in regulating whether human activities expand or shrink, or speed up or slow down. Areas with decreasing heterogeneity are predicted to exhibit greater rates of expansion due to greater connectivity. Given the way human activities are decreasing heterogeneity among many regions (Steele *et al.* 2014; Hall *et al.* 2016), expansion processes may become more common than shrinking processes. However, if decreasing heterogeneity results in a reduction in cover type that impedes connectivity, decreasing heterogeneity may slow down processes such as dispersal or migration. Therefore, heterogeneity may benefit some processes and be a detriment to others.

Testing the *STAR hypothesis* is predicated on research programmes capable of detecting macroscale processes and changes by making appropriately scaled measurements. Fortunately, there are several efforts that are well suited to address this hypothesis. For example, satellite remote sensing can provide near global coverage of ecosystems at temporal scales approaching daily, and thus are well suited to assessing predicted “expanding” and “shrinking” interactions. Meanwhile, long-term ecological research programmes provide place-based records well suited to interpreting ecological interactions that

are “speeding up” and “slowing down”. Finally, research programmes like the US National Ecological Observatory Network (NEON) may provide the capability to cover both large spatial extents and up to decadal time periods, at spatially and temporally fine scales. In addition, new approaches and technologies have emerged that greatly facilitate observing, measuring and analysing biological, geophysical and human phenomena across multiple spatial extents (Michener & Jones 2012; Levy *et al.* 2014; Pace *et al.* 2015).

A key challenge to producing macrosystem-scale ecological insights is addressing the importance and implications of heterogeneity in regulating variable scaling rules governing ecological interactions across space and time. Research conducted in landscapes has demonstrated that spatial pattern and heterogeneity are often key to understanding ecological processes and should not be ignored. A key challenge is thus understanding when heterogeneity is likely to be an important factor influencing the scaling of processes, mechanisms or phenomena across space and time works, and just as importantly, when does it not (Turner & Gardner 2015). In addition, while human activities are decreasing heterogeneity in many regions (Steele *et al.* 2014; Hall *et al.* 2016), ecological novelty is also being created via new combinations of interacting physical, chemical and biological characteristics (Keuffer *et al.* 2014). The seeming opposing changes in decreasing ecological heterogeneity in space but increasing novelty through time highlight a complexity imbedded in understanding the implications of ecological change at macrosystem scales.

Some of the most important social and ecological challenges occur at the broadest spatial scales. Macrosystems ecology is poised to serve as a leading intellectual framework in understanding and providing solution options to some of the most perplexing and ‘wicked’ environmental dilemmas. To deliver on this potential will require that macrosystems ecology is successful in building on the key intellectual foundations underpinning it, while also revising and refining core hypotheses as new knowledge is produced. Doing so will enable macrosystems ecology to provide both great scientific and societal value for many years to come.

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