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SYNTHESIS & INTEGRATION

A framework for lotic macrosystem research

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Abstract. We analyze here the nature of research in freshwater macrosystem biology (especially lotic studies) from both conceptual and current research perspectives. The boundaries of permanent and transitional lotic macrosystems from the smallest to largest spatial extents are described. We contrast ecosystem vs. macrosystem research and macroecology vs. macrosystems ecology and provide some examples of representative aquatic macrosystems ecology projects in the USA. We recommend approaches for incorporating certain large-scale lotic concepts developed over the last 40 yr as the bases for lotic macrosystem studies. Of these, the three most appropriate in chronological order are the River Continuum Concept, the Riverine Ecosystem Synthesis, and the Stream Biome Gradient Concept. Four other concepts would be suitable for testing macrosystem hypotheses after incorporating small to large conceptual or geographic expansions of the models. We suggest future research directions in lotic macrosystem research in areas of climate change and teleconnections among distant organisms and systems and include general recommendations for conducting macrosystem-level research.

Key words: ecosystem ecology; macroecology; macrosystem ecology; stream ecology concepts; teleconnections.

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Introduction

Macrosystem biology is a discipline focused at large spatial scales, such as whole ecoregions, biomes, or continental comparisons (Heffernan et al. 2014). Research at macrosystem scales is still relatively rare but has begun to accelerate substantially over the last decades on several continents, including the large European Danube River project (see the International Commission for the Protection of the Danube River). Such studies increased dramatically in the USA in the last decade when the U.S. National Science Foundation (NSF) established an ecological program (Gholz and Blood 2016) to promote large-scale research in ecology. Such research could potentially involve biotic and abiotic interactions at large spatial and sometimes temporal scales, with the latter focused mostly on climate changes. The macrosystem biology program (MSB; or macrosystem ecology) at NSF was recently linked with the National Environmental Observatory Network (NEON) to provide a suite of environmental climatic data to promote macrosystem research in aquatic and terrestrial systems.

Macrosystem ecology generally builds on current ecological knowledge of processes occurring at large scales by extending the spatial extent of the study (LaRue et al. 2021) while also incorporating effects of climatic processes and both natural and anthropogenic environmental interactions occurring over long distances (teleconnections; Tromboni et al. 2021). The uniqueness of this approach is not in developing new scientific techniques but instead is demonstrated by the types of research questions posed and the way that multiple, common ecological techniques are combined in one study at large spatial scales. Macrosystem research is often conducted at spatial scales where humans impact the environment and alter broad-scale ecosystem services. Thus, the research has important relevance for developing environmental policies that lead toward the sustainability of nature.

To move the field of lotic macrosystem research forward, it is vital that we avoid simply renaming past concepts or creating completely new frameworks when modifications of, and merger with existing theories would be more appropriate. To meet these objectives, this manuscript is focused on the following four questions as they relate in particular to lotic macrosystem research throughout the world: (1) What constitutes a lotic macrosystem? (2) What are the differences between macrosystem ecology and the related fields of both macroecology and ecosystem ecology, and what are especially relevant examples of recent approaches in macrosystems ecology? (3) How could we employ and possibly expand current lotic concepts as platforms for conducting future macrosystem studies? And (4) which components of aquatic macrosystem research especially require additional research.

The Spatial Extent and Research Foci of Lotic Macrosystem Ecology

While scientists often feel the need to categorize and delineate, this does not always represent the true state of the natural world. For example, it is always difficult for scientists to establish definitive spatial and conceptual boundaries of stream reaches, rivers, communities, or ecosystems. Similarly, we do not expect consistency in either delineating the boundaries of a lotic macrosystem or in defining what constitutes macrosystem research. Rather, in the current paper we hope to provide a general sense of how the macrosystem framework applies to lotic ecosystems and how it might provide new insights.

The boundaries of lotic macrosystem studies could be defined in various ways, such as (1) an array of permanent or intermittent streams at multiple, unconnected geographic locations; (2) a series of adjacent, whole river watersheds that directly connect with the ocean (e.g., coastal rivers along the Gulf of Mexico and various rivers flowing into the Mediterranean Sea); or perhaps; and (3) a large watershed composed of many individual tributary rivers characterized by different ecoregions (and sometimes biomes), elevations, geologies, landscape features, and/or human impacts (e.g., the Amazon, Danube, Mekong, Mississippi, Murray–Darling, and Nile Rivers). The Carson River watershed in the U.S. states of eastern California and northwestern Nevada could be classified as a single river ecosystem, while the Carson, Humboldt, Bear, and Weber Rivers together could be defined as a macrosystem group within the U.S. Great Basin, with all of these rivers having high elevation, forested headwaters and lowland semi-arid steppes in endorheic basins. In contrast, large rivers are rare compared to headwater streams, and thus, they pose replication and sampling challenges in macrosystem studies. However, research on entire watersheds and channels of a single river draining a very large basin—such as the Mississippi or Danube Rivers—could be considered a single macrosystem study if such a river integrates large stream networks passing through multiple ecoregions and even biomes.

Macrosystems could also include ecosystems that transition between lentic and lotic ecosystems. For example, the Kherlen River of eastern Mongolia flows into Lake Hulun (or Dalai Lake), where it becomes a lentic system for a short time period and distance. In years of higher precipitation and river discharge, however, Lake Hulun essentially becomes a fluvial lake that allows the Kherlen to flow into the Amur River and then to the Pacific Ocean—presumably with extensive ecological implications. Additionally, the Tonlé Sap system in Cambodia is a seasonally inundated lake–river which connects with the Mekong River. Studying transitional lentic–lotic systems could provide useful insights into macrosystem processes.

The nature of lotic macrosystem studies could vary with the spatial extent of the system. Research in macrosystem ecology in its smallest spatial extent could involve studies of a large portion of a river or even the entire watershed as it passes through multiple ecoregions. Such an approach would allow a nested, hierarchical spatial analyses at the spatial extent of macrosystems. This contrasts with community and ecosystem studies (e.g., system metabolism or nutrient spiraling studies) at the valley or even reach levels. Macrosystem studies at their largest spatial extent could involve research on multiple rivers in entirely separate watersheds located in different biomes or in the same type of biome but on different continents. For example, our team studied ecological processes from system metabolism to fish traits in three different ecoregions of the temperate steppe biomes of the USA and Mongolia. Studies of macrosystem ecology increasingly diverge from community and ecosystem ecology with increases in the number of dependent variables, ecological techniques, and both ecoregional variability and distances among sites.

There are specific differences between ecosystem and macrosystem research as described in Table 1. Note that common spatial boundaries of ecosystems and macrosystems provide few clues to the nature and breadth of their research foci. Both might encompass an entire watershed spatially, but the research focus may be broad or finite.

Macrosystem Ecology vs. Macroecology

Macrosystems ecology (sometimes called macrosystems biology) overlaps extensively with the field of macroecology because both focus on processes and/or species distributions occurring over large spatial extents (ecoregional to continental scales). However, macrosystems ecology typically extends from community to ecosystem properties, while macroecology generally emphasizes population to community processes and has close associations with biogeography (Loreau et al. 2003). Our perspectives on macrosystems ecology apply to some macroecological studies (cf. Brown and Maurer 1989). While both macroecology and macrosystem ecology focus on large geographic scales (McCluney et al. 2014, Thorp 2014), the latter integrates dependent variables ranging from community functional traits through whole ecosystem processes and effects of large-scale drivers. In a sense, we view macroecology as one branch of macrosystems ecology. Macrosystem ecology adds interactions and feedbacks among units across spatial scales, with an emphasis on interactions between one or more biological, geophysical, and sometimes socio-cultural components (Heffernan et al. 2014, Levy 2014, Fei et al. 2016). Ecoregional classifications (e.g., nutrient ecoregions; Omernik 1987, Abell 2008) can serve as independent variables for use in some macrosystem studies even though these units usually focus on only one ecological response variable (e.g., baseline nutrients, unique vertebrate taxonomy). In summary, the scientific overlap between these two disciplines is significant; however, macrosystem ecology includes some areas that have not traditionally been studied in macroecology, such as ecosystem processes at very large scales, consideration of teleconnections, and more detailed consideration of anthropogenic impacts and responses (as evidenced in the next section).

Examples of Macrosystem Research Funded by the U.S. NSF

Some examples of freshwater macrosystem projects that have been funded by the U.S. National Science Foundation and undertaken in the last decade include (1) development of a freshwater nutrient database for major lakes across a continent (NSF Award 1638679; Soranno et al.); (2) a study of climate and land-use effects on waterfowl and amphibians in wetlands of

Table 1. Types of lotic studies with a comparison of ecosystem vs. macrosystem research and different types of macrosystem studies.

Characteristic	Ecosystem research project	Macrosystem research projects across multiple ecosystems		
		Type 1	Type 2	Type 3
Lotic systems	Single river basin	Small stream sections in many rivers of multiple ecoregions or biomes	One very large river basin passing through multiple ecoregions or biomes	Many whole river basins in different ecoregions or biomes
Spatial research category	Single river basin with sampling in one or more stream orders	One to a few stream orders but in multiple streams and watersheds	Sampling many stream orders within a large basin consisting of many rivers in different ecoregions	Multiple independent (unconnected) watersheds in similar types of ecoregions or biomes
Examples of lotic rivers on various continents	AU: Cooper Creek; EU: River Tweed; NA: Kanawha River; SA: Rio Traful	Similar stream order in rivers of different ecoregions or biomes	EU: Rhine River; NA: Mississippi River; AS: Mekong River or large sub-basins	Rivers from different basins in different biomes or ecoregions, such as those on the U.S. West Coast
Breadth of dependent variables	Usually system metabolism and elemental cycling in multiple stream orders	A few biotic traits or processes in one or more orders of multiple rivers	One to many of the same dependent variables in one or more stream orders throughout the basin	One to many dependent variables present in multiple stream orders of each river

temperate steppes (NSF 1340413; Johnson et al.); (3) comparison of macroinvertebrates in perennial and permanent streams in ten ecoregions (NSF 1802872; Allen et al.); (4) research on dissolved organic matter fluxes in headwater streams of a single moderate sized basin, Connecticut River (NSF 1340749; Raymond et al.); (5) a survey of annual metabolism measurements in streams across North America to initiate the development of a half-century database (NSF 1442467; Stanley et al.); (6) an analysis of the effects on community and genetic composition of large branchiopods (fairy and tadpole shrimps) in ephemeral wetlands of a grassland biome from teleconnections via wind and waterfowl (NSF 1926596; Thorp et al.); and (7) an examination of the effects of ecoregion and hydrogeomorphology on system metabolism, and the diversity, traits, and food webs of fishes and invertebrate assemblages in temperate steppe biomes of the USA and Mongolia (NSF 1442595; Thorp et al.). Analytical techniques in most of these projects have not differed substantially from research at smaller spatial extents (with the possible exception of the use of large-scale imagery and spatial geographical information system analyses), and thus, one might ask: "How is this approach different from previous community and ecosystem studies in other rivers?" While scientific methods may have been similar, in most instances current and recent macrosystem projects have spanned greater geographical and ecological areas and have compared data within and among individual ecosystems to interpret processes occurring at larger spatial scales.

Integrating Current Lotic Concepts into Macrosystem Studies

Rather than entirely reinventing the wheel in lotic macrosystem studies with new concepts, it is worth examining whether and how we can integrate past concepts to incorporate a macrosystem approach. Many influential ecological concepts have been proposed in lotic research, but only a limited number characterize watersheds from headwaters to large rivers and thus emphasize sufficiently large spatial extents to allow easy modification into a macrosystem framework. The smaller scale concepts can then serve as useful building blocks in a larger macrosystem ecology framework. Such concepts, such as those shown in Fig. 1, are especially useful when they are driven by basic hydrogeomorphic and/or terrestrial (e.g., catchment vegetation) interactions with lotic structure and function and can therefore be connected to large-scale regional-to-global drivers of those hydrogeomorphic and terrestrial characteristics. The published concepts summarized below vary in how they classify the geomorphic structure of rivers, although many rely to some extent on the physical model of rivers described by

Frissell et al. (1986) and earlier studies by Leopold et al. (1964). Other prominent lotic concepts that focused on more limited dependent variables, such as carbon sources in food webs (e.g., Junk et al. 1989, Thorp and Delong 2002, Humphries et al. 2014), could certainly contribute to analyses of dependent variables in macrosystem studies, especially if spatially expanded, but are not evaluated in the current manuscript as comprehensive macrosystem frameworks. Note that we are not evaluating the quality of the concepts but instead merely the ease by which they can serve to construct a framework for macrosystem studies.

The three concepts we argue are most easily applied or modified for a lotic macrosystem ecology study are (by publication date): the River Continuum Concept (RCC; Vannote et al. 1980), the Riverine Ecosystem Synthesis (RES; Thorp et al. 2006, 2008), and the Stream Biome Gradient Concept (SBGC; Dodds et al. 2015).

The original RCC paper focused on predicted, clinal (continuous) changes in energetics, species composition, and food sources in main channels from forested headwaters downstream to the river's outlet. It was later modified by Sedell et al. (1989) to focus on inputs from floodplains in large rivers following publication of the Flood Pulse Concept of Junk et al. (1989) and applied to temperate steppe biomes by Dodds et al. (2004). To expand the RCC as a macrosystem concept, it could incorporate effects of lateral (slackwater) components of the riverscape and floodscape, tributary structure, and main channel hydrogeomorphology (cf. Leopold et al. 1964, Bruns et al. 1984, Perry and Schaeffer 1987, Montgomery 1999). It could also be modified to account for rivers that move across biomes and expanded to more specific biomes (e.g., desert or tundra streams).

The RES compared ecological effects of site location from headwaters to a river's mouth using reach (or micro-valley) to valley scale hydrogeomorphic units (functional process zones, or FPZs), and it described testable ecological hypotheses/tenets from population to landscape levels (Thorp et al. 2006, 2008). This has particular relevance to macrosystem approaches

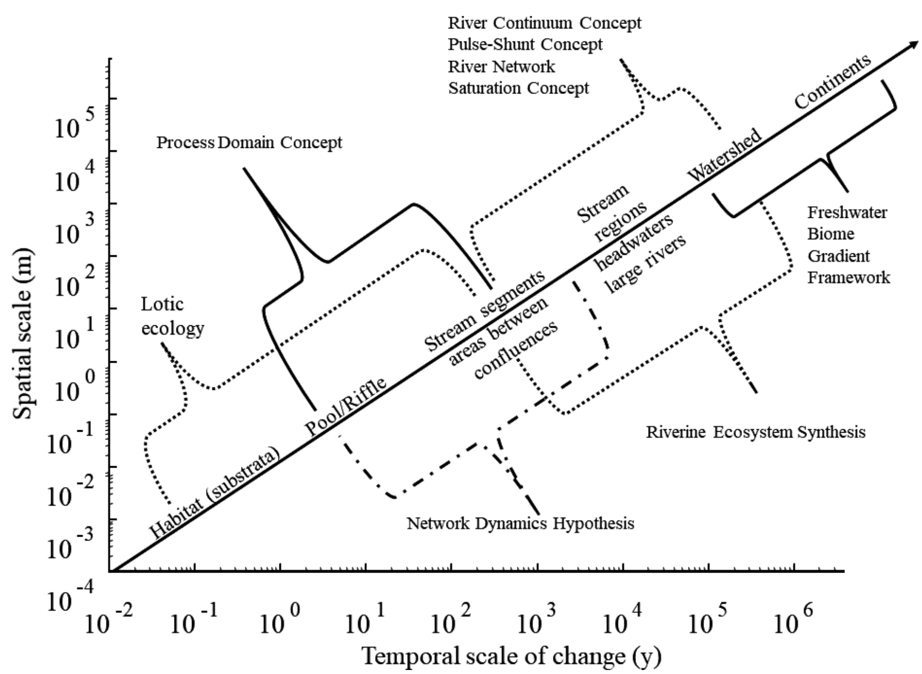

Fig. 1. This figure is one view of how published lotic concepts relate to spatial and temporal gradients. We acknowledge that the placement of these concepts on both axes is based only on our consensus perception of their position and may not reflect the intentions of the original authors of these concepts.

because differences in FPZs specifically depend on the whole macrosystem context, and their importance also relies upon the degree of connection and location within that system. Shown in Fig. 2 are examples of distinct but contiguous FPZs which could be characterized by different ecological structure and function. Pre-identified FPZs (Thoms and Parsons 2003, Thorp et al. 2013, Williams et al. 2013) in multiple watersheds could serve as independent variables for examining effects of basin characteristics, hydrogeomorphic form, and downstream distribution on many ecological processes across broad spatial and temporal scales (Maasri et al. 2018, 2019). The latter could include studies of within-site stability and asynchrony as well as their possible ecological portfolio effects.

The SBGC (and expanded as the Freshwater Biome Gradient Framework; Dodds et al. 2019) explicitly used a macrosystem approach and emphasized strong effects of climate on stream communities and ecosystem properties from the influence of temperature and precipitation on hydrology and geomorphology (cf., Poff et al. 1997, Allan and Castillo 2007), with terrestrial vegetation indirectly mediating this relationship. It also considered other factors that can vary as a function of latitude or elevation, such as light intensity and geomorphology. The SBGC emphasized strong effects of climate on community structure and function through a stream's disturbance and flow regimes, sediment load, temperature, and light availability. This basic dependence of streams on climate may enable investigators to predict the nature of a stream's biotic structure and ecological function across desert to forest biomes even in poorly studied biomes and in urban streams (Hale et al. 2016).

In addition to the three concepts discussed above that can be easily modified or employed directly to study lotic macrosystems, four other concepts are valuable in their own right but seem to require more modification than the previous three to enhance their applicability to macrosystem studies. These are (1) the Process Domain Concept (PDC; Montgomery 1999); (2) the Network Dynamics Hypothesis (NDH; Benda et al. 2004); and (3) the combined Pulse-Shunt Concept (PSC; Raymond et al. 2016) and River Network Saturation Concept (RNS; Wollheim et al. 2018). The PDC was proposed as an alternative or finer-scale supplement to the RCC. It emphasized the importance of geomorphic processes and litho-topo units to community structure and dynamics as a partial result of distinctly different disturbance regimes. The landscape view of the NDH is focused on the hierarchical nature of branching river networks and their interactions with watershed disturbances (fires, storms, and floods) that imposed a non-uniform distribution of riverine habitats, with consequences for biological diversity and productivity. The PSC and RNS collectively provided a conceptual framework for linking catchment hydrology with terrestrial to aquatic biogeochemical fluxes at a whole river network scale, emphasizing links between flow and both material transport and processing. Such approaches could be extremely useful in a macrosystems framework as they specifically consider spatial arrangement and connection of subsystems in a watershed. The PSC and RNSC provided a network scale extension of the nutrient spiraling concept (Newbold et al. 1981, Ensign and Doyle 2006) that was tightly linked to landscapes and which explicitly acknowledged broad-scale source–sink dynamics in lotic systems.

Some Lotic Research Needs in Macrosystem Ecology

Although many aquatic macrosystems would benefit from ecological analyses with only minor modification in current scientific approaches, some particularly new and challenging aspects of macrosystem ecology await our attention. These include the role of temporal variability and long-distance interactions on macrosystem structure and functioning over time. Although GIS contributes to these research needs for niche modeling in ecological and evolutionary applications (Peterson 2003, Kozak et al. 2008), we suggest that macrosystem ecology is more comprehensive.

Climate change

Trends over space and time in the biotic structure and ecological function of aquatic systems are widely observed in nature, but the actual drivers of temporal variability in macrosystems that feature prominent spatial diversity are not well understood even though the ecological effects

Fig. 2. Two adjacent, upland hydrogeomorphic zones (functional process zones, or FPZs) in the Carson River of California and Nevada, USA which were sampled as part of our NSF macrosystem biology project: (a) upland, high energy site; and (b) upland low energy site immediately located below the high energy site.

are expected to be widespread. These phenomena have implications for understanding basic ecological processes, conserving threatened species, reducing overall anthropogenic impacts, and sustaining human welfare and economies (Patrick et al. 2021). Given that population fluctuations may be exaggerated by climate change, thereby increasing the risk of extinctions to local and global populations of certain species (e.g., Schindler et al. 2010), it is increasingly important that we both understand synchronous and asynchronous responses of components within macrosystems to climatic variability at large spatial scales and comprehend how biodiversity is related to macrosystem functioning (cf. Gonzalez et al. 2020). For example, in a recent macrosystem study of rivers in similar latitudes of two temperate steppe biomes, we compared ecological processes in rivers of Mongolia and USA, with the former being subjected to air temperate changes (an 1.8°C increase over a recent 40-yr period; Nandintsetseg et al. 2007) which are three times faster than the overall average for the northern hemisphere and which represents one of the strongest warming signals on earth (Chase et al. 2000). The geographic span of large-scale macrosystem studies offers unique opportunities to understand and possibly better predict effects of climate changes in similar macrosystems on other continents.

Teleconnections

An important but largely theoretical component of macrosystem ecology involves (1) interactions among distant macrosystems characterized by teleconnections (climatic effects or certain species interactions); (2) enhanced or diminished, macroscale feedbacks; (3) humans as drivers that may operate across broad spatial extents; and/or (4) cross-scale interactions (phenomena at one spatiotemporal scale affecting processes primarily operating at another scale; e.g., Heffernan et al. 2014, Soranno 2014, Liu et al. 2015, Tromboni et al. 2021).

Interactions among ecosystems and macrosystems could occur between adjacent or at least nearby systems (pericoupling) or distant locations (telecoupling; e.g., Liu 2017, Tromboni et al. 2021). A proposed metacoupling framework integrates nearby-to-distant interactions and encompasses both natural and anthropogenic processes (Liu 2017, Tromboni et al. 2021). Natural teleconnections could include, for example, intercontinental dispersal of rotifers and other zooplankton embryos via wind as well as dispersal of embryos of large branchiopods (e.g., fairy and tadpole shrimps) between northern and southern portions of the U.S. Great Plains by wind and waterfowl (on feathers and in the gut). Such natural phenomena are relatively easy to predict. Often harder to predict are effects of invasive species because investigators do not know when and where they will arrive, and whether their competitive abilities will be the same in a different part of the world. For example, with past policies on the discharge of ship ballast water, it was not hard to predict via telecoupling the eventual arrival into North American waters of zebra and quagga mussels (*Dreissena* spp.) in ships traveling from Europe (Thorp et al. 1994). Given that these bivalves occupied a known niche (a planktivorous mussel attached by byssal threads to hard surfaces like rocks, wood, and shells of native mussels; Thorp et al. 1998) that was essentially unique within North American freshwaters, their eventual spread through much of the USA via pericoupling in lotic and lentic habitats was not surprising, which is unlike the case for many potential invaders.

Suggested research

We recommend that ecologists interested in either basic or natural aspects of lotic macrosystems adopt or expand two basic research approaches. For studies of climate change, ecologists could conduct comparative field studies of ecological processes in different latitudes of a single continent combined with carefully controlled experiments on possible ecological changes potentially wrought by likely future invaders responding to new climatic conditions. Alternatively or in addition, potential climate-induced changes in macrosystem processes could be studied at the same latitudes but on different continents where responses to climate changes could be different (e.g., our studies of rivers in the USA and Mongolia). Expansion of ongoing and new studies of the ecosystem effects of potential invasive species should include analyses of likely teleconnection pathways peculiar to groups of species and analyses of niche characteristics of species and communities to predict likely openings for invasion. Historical data on changes in environmental variables and community composition through time can be important, including changes in species composition and presence of invasive species, as could studies of processes in similar macrosystems distributed among different climatic zones. Many of these approaches will require international cooperation of scientists and governments, possibly with a new international organization to promote these studies.

Goals of this Paper and Summary

Four goals of this paper were described at the end of the *Introduction*, and our general conclusions and recommendations are summarized here. (1) The nature of a lotic macrosystem has been shown to be larger than a single ecosystem and typically involves multiple ecoregions and sometimes biomes. Some differences between ecosystem and macrosystem research are illustrated in Table 1. (2) Macrosystem ecology, macroecology, and ecosystem ecology overlap in techniques, but the first two typically involve significantly larger spatial extents. Macroecology emphasizes questions related to population and community ecology, while macrosystems ecology focuses on questions from community ecology (especially traits) through ecosystem ecology. (3) Specific recommendations for expanding three current lotic theories as macrosystem concepts are described for the RCC (Vannote et al. 1980), the RES (Thorp et al. 2006, 2008) and the SBGC (Dodds et al. 2015). (4) Our recommendations for future macrosystem research are described below in the final section of this paper.

General Recommendations for Lotic Macrosystem Studies

A primary goal of macrosystem studies should be the pursuit of generality and an escape from local (spatial) and recent (temporal) contingencies (McGill 2019). It follows that these studies should place an emphasis on hierarchical scaling and occur over broad spatial and/or temporal scales, with temporal interactions significant over decades to millennia (Thorp 2014). While we recognize that generality at large spatial scales could miss contingencies important at smaller scales, the relevance of large-scale ecology to major environmental issues requires a large-scale viewpoint. Macrosystem studies that are short in duration should occur on spatial scales where the major factors are consistent over decadal to millennial time scales to reduce significant temporal contingency (Allen and Starr 2017). To obtain the most comprehensive analyses of the functioning of rivers, investigators will likely need to concentrate on common broad-scale features that preeminently characterize all aquatic systems, such as hydrologic regime, geomorphology, and myriad terrestrial influences. At the community level, the focus should be on the study of traits and not only the distribution of individual species. Macrosystem studies could also benefit from previous, independent studies by collating data from many small-scale studies to find common, non-contingent threads that lead to ecological generalizations.

When making comparisons among rivers (a key component of macrosystem ecology), researchers should account for inter- and intra-river differences in (1) basin characteristics (geology, topography, and land cover; especially riparian conditions); (2) climate (historic, current, and future projections); (3) human impacts (e.g., dams, agriculture, and urban effects); (4) season of study (focus on periods of high productivity if time is limited); (5) stream characteristics, such as hydrogeomorphology, channel structure (including lateral channels), and substrate characteristics; and (6) hydrology (including stream depth, current velocities, discharge patterns, and flood regimes and history).

We in no way propose that macrosystems ecology will replace or assume more importance than smaller scale studies, field experiments, natural history, monitoring, or the many other more traditional approaches to understanding lotic ecology. All the approaches will be necessary ingredients to successful macroscale approaches. We view macrosystem approaches as giving more context to the generality of results obtained from smaller scale research and allowing scientists to help understand and possibly solve environmental problems that are increasingly global in their nature and manifestations.

Macrosystem research will be improved by emphasizing the dynamism of ecological systems, by incorporating individual strengths of sometimes disparate ecological concepts, and by imbuing our studies with the exhilarating sense gained from exploring new frontiers rather than being overly mired in defending past concepts.

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