Macrosystems revisited: challenges and successes in a new subdiscipline of ecology

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Macrosystems biology research has expanded and evolved over the past decade as the scientific community grapples with ecological issues at regional to continental scales relevant to human interactions within the biosphere. Macrosystems biology builds on established fields of study like population and community ecology, biogeography, and global biogeochemistry, and has the potential to develop into a unique and important subdiscipline. If we achieve this outcome, macrosystems research will likely have increasing relevance to ecological science and its practical application, and could potentially transform large-scale ecological understanding. Both previous studies and the articles included in this Special Issue document the development of a broad spectrum of macrosystems approaches, how ecological researchers have accommodated the sociological aspects of collaboration among diverse individuals and groups, and how new methods are being applied to deal with the large and diverse types of data used by macrosystems biologists.

In a nutshell:
- Macrosystems biology is a relatively new field of ecological research that explicitly considers large-scale (e.g., regional, continental, biosphere-level) complex systems in a framework of ecological processes and patterns
- This new approach is particularly relevant to ecosystem services, including environmental quality, and the conservation of biodiversity
- The study of macrosystems, which began prior to the naming of the subdiscipline and formal programmatic funding, fills a unique and growing niche in ecological research
- The influence of macrosystems biology is expanding due to its unique contributions, large-scale and multidisciplinary approaches, and increasing relevance of research outputs

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Macrosystems biology has now been a formal NSF program (albeit under an evolving array of titles) for 10 years (as of mid-2020). A key event that catalyzed the nucleation of macrosystems biology as a subdiscipline was a previous Special Issue (“Macrosystems Ecology – an emerging perspective”, published in 2014) in *Frontiers in Ecology and the Environment*, which outlined the potential of the approach (Soranno and Schimel 2014). That Special Issue provided an initial definition of macrosystems biology (Heffernan et al. 2014) and suggested future directions for and challenges to the field (e.g. Rüegg et al. 2014). A second special issue published in the journal *Landscape Ecology* in 2016 (Fei et al. 2016) highlighted novel methods and new insights generated from macrosystems biology research. Several publications have since contributed to the refinement of macrosystems biology thinking (e.g. Rose et al. 2017).

Here, we describe the new perspectives gained from macrosystems research and training by highlighting the main points of the articles included in this Special Issue and emphasizing some of the accomplishments of macrosystems biology research from other peer-reviewed publications. We first reflect on the intellectual overlap of macrosystems biology with other past and present fields of research, building on the quantitative literature analysis presented by LaRue et al. (2021). We consider how the articles published here exemplify the diversity of approaches that macrosystems research has necessitated, and the diversity of results that it has made possible. A clear picture emerges that macrosystems biology is more than just science associated with NEON. Finally, we explore the possible future of macrosystems biology and the promise of the approach for generating novel insights into natural processes.

**General characteristics of macrosystems research**

Research relating to macrosystems biology spans a diversity of focal ecosystems, spatial scales, and methods. Macrosystems biology is not necessarily a new approach, as many prior and ongoing initiatives fall under the definition given in the introduction (see below). Given the spatial scale of macrosystems biology research, projects are often – though not always – large and complex, and typically involve collaborators from multiple institutions and disciplines (e.g. ecology, geology, economics, computer science, among many others). Projects generally fall into one of three categories. First, and arguably the most common type, are projects that generate new estimates of patterns and processes at very large spatial scales. For example, Song et al. (2018) compiled measurements of stream metabolism across North America to predict the consequences of climate change on primary production and respiration as part of the Scale, Consumers, and Lotic Ecosystem Rates project. This study involved analysis of comparable experiments at many sites across the continent and was composed of a large, multi-institutional group of scientists (Figure 1). Similarly, Iannone et al. (2015) estimated forest invasion richness and abundance at sites spanning the entire continental US and identified key factors associated with plant invasions.

The second category of macrosystems biological research addresses questions that integrate information from monitoring networks and large-scale data compilation efforts. This use of data has enabled projects that leverage new technological or methodological abilities to test foundational theories or long-existing hypotheses related to large-scale ecological patterns. Many hypotheses deriving from historical observations or modest datasets were untestable when originally conceived because the technology that existed at the time was inadequate to extrapolate research results from a few locations to continental or global scales. For example, there are latitudinal gradients in biodiversity that have historically resisted definitive explanation (Davies et al. 2011), but macrosystems biology approaches offer new insights. Fei et al. (2018), for instance, demonstrated that the biodiversity–productivity relationship changes across a large spatial extent, with climatic variation as the underlying determinant, while Read et al. (2018) used continental-scale monitoring of small mammal populations to demonstrate how trait space can explain increased diversity at lower latitudes. Macrosystems biology is also poised to test other long-standing hypotheses, such as scaling interactions across the regional and global biosphere (see Ballantyne et al. 2021). Contemporary tools (e.g. national and independent sensor networks, remote sensing, citizen-science programs) provide new opportunities for assessing previously untestable concepts and hypotheses.

The third category of projects consists of research that suggests that at least some macrosystems projects are not easily definable (see Rose et al. 2017). For example, teleconnections represent one novel area of research that can help explain broad-scale patterns and processes (Heffernan et al. 2014). Tromboni et al. (2021; also discussed in greater detail below) explain how teleconnections (remote effects on local systems) can have strong ecological and sociological implications, and detail how humans acting at large scales can transmit actions to otherwise unconnected ecosystems. In addition, integrating macroscale biology research with sociological approaches represents a unique combination that should generate original and useful results.

**Examples suggesting macrosystems biology existed as a field before the name was coined**

Research at large scales is not new, nor is funding for such projects from other sources. For example, the US National Aeronautics and Space Administration (NASA) Terrestrial
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Macrosystems is developing as a scientific discipline

Macrosystems biology is rapidly becoming a distinct subdiscipline of ecology, in which ideas and connections across diverse disciplinary boundaries generate insights with societal relevance. Articles in this Special Issue underscore these points; some societally relevant topics include understanding C cycling across large to small spatial scales at a time when atmospheric concentrations of carbon dioxide (CO₂) are exceedingly high (Ballantyne et al. 2021), and the maintenance of biodiversity is coupled to an understanding of the stability of ecosystems (Patrick et al. 2021). Ballantyne et al. (2021) present the well-known challenges to improving knowledge of CO₂ loss pathways (other than respiration) and reconciling the large differences in estimates of C uptake rates generated by “scaled-up” eddy flux measurements with those generated by Earth system models. The authors suggest that this problem could be resolved through a better understanding of C balance at the macrosystem biome scale considering plant functional types, which could yield a richer understanding of C-cycling processes. In addition, they highlight opportunities to combine observations across ecosystems to expand knowledge about regional to global changes in atmospheric gas composition, vapor pressure, surface temperatures, and regional precipitation. Their approach builds on related studies that suggest understanding ecosystem responses in macrosystems requires large-scale

Figure 1. Stream metabolism chambers used to standardize measurement of metabolic characteristics at sites across the North American continent, from (a) the North Slope of Alaska to (b) Puerto Rico. (c) Broadly distributed geographic projects such as these require large and diverse teams of researchers.

Ecology program funds large-scale research using remote sensing along with field research and modeling to elucidate ecosystem functions; the US Department of Energy (DoE) Terrestrial Ecosystems Science Program also focuses on large-scale carbon (C), water, and nutrient cycling; and the International Long Term Ecological Research Network (ILTER), which consists of a network of long-term ecological sites, is funded by several countries.

Several prior efforts and initiatives (ecological observation or experimental networks) suggest that modern macrosystems approaches have existed prior to the subdiscipline having a formal name. A few of the many programs include (1) the Nutrient Network, a globally distributed fertilization experiment in terrestrial herbaceous habitats (Borer et al. 2014); (2) the International Tundra Experiment, a warming experiment involving 61 tundra sites (Elmendorf et al. 2012); (3) the Long-Term Intersite Decomposition Experiment Team (LIDET), a litter decomposition experiment involving 27 sites across North America (Harmon et al. 2009); (4) the Biodiversity and Ecological Processes in Terrestrial Herbaceous ecosystems program, a cross-European plant diversity manipulation experiment (Hector et al. 1999); and (5) RivFunction, a European network of 200 sites focusing on stream detritus decomposition (Chauvet et al. 2016). The geographic extent of several of these networks is depicted in Figure 2.

Two additional efforts illustrative of antecedent grassroots-level macrosystems approaches include the Global Lake Ecological Observatory Network (GLEON) and the earlier Lotic Intersite Nitrogen Experiment (LINX). These programs illustrate the success of research involving large spatial scales, as well as the associated challenges of information management, data sharing, and group dynamics in projects involving extensive collaboration.

The LINX project, which began in 1995, consisted of two continental-scale experiments conducted over 17 years. The experiments used nitrogen-15 (¹⁵N) tracers to establish N cycling rates and movement throughout food webs (LINX collaborators 2014), and were conducted at multiple sites across North America (from Puerto Rico to Alaska) using a standardized methodology. The research ultimately enabled large-scale predictions concerning the effects of land use on N retention in streams and the global rate of nitrous oxide released from streams.

GLEON, initiated in 2004, is a grassroots network of people, data, and observatories (Rose et al. 2016). The primary goal of the program is to improve understanding, conservation, and predictions of the state of lakes and reservoirs globally by bringing together a diverse community of scientists, engineers, information technology experts, and engaged stakeholders (Weathers et al. 2013). This large-scale, synthetic ecological approach is consistent with definitions of macrosystems biology and has generated a range of scientific, educational, and outreach products, including software tools, scientific publications, and educational modules and programs.
approaches, and that variation among and within regions is important.

Understanding the drivers and maintenance of biodiversity has long been a primary focus of ecological research, and is of particular interest to ecosystem managers given the current rapid decline in global and regional biodiversity. Patrick et al. (2021) discuss the ways in which preservation of regional biodiversity links to the temporal stability of the macrosystem, and highlight how processes interacting within and among habitats contribute to stability of a broader, regional macrosystem. They propose and test a theoretical framework regarding the drivers of animal and plant biomass and abundance in relation to the variability of ecosystem traits in space and time, and present case studies indicating that biodiversity levels within local communities and at regional scales for different ecosystems are common factors that likely influence the stability of the regional macrosystem.

Socioecological connections can also drive ecosystem changes. Traditional approaches have rarely considered connections over large spatial and temporal scales influencing the environment, leading Tromboni et al. (2021) to propose application of a “metacoupling” framework to characterize subsystem coupling driving ecological dynamics. The authors employ case studies to illustrate how consideration of connections among macrosystems can expand understanding of patterns at regional to continental scales. They show that distant interactions can at times be stronger than adjacent ones, and that human activities often alter temporal dynamics and magnify the relevance of distant interactions. These long-distance interactions may be of vital importance to managers of subscale (local) systems for understanding the causes and implications of environmental change. Finally, feedbacks between metacoupled systems can modify both systems, thereby changing the broader regional system.

The articles included in this Special Issue also discuss how macrosystems research can be integrated with and enriches other fields of study, for example by addressing the challenges associated with nonstationarity (a stochastic process whose unconditional joint probability distribution is a function of time), combining data across scales, and training large collaborative groups. Nonstationarity is a common feature of ecological systems as they change over time, violating statistical assumptions, and is particularly a problem in analyses of large spatial scale data (Rollinson et al. 2021). Statistical approaches that are insensitive to nonstationarity are important to macrosystems biologists as well as to the broader community of ecologists faced with similar statistical problems, and as such, Rollinson et al. (2021) summarize challenges and solutions relevant to all ecologists. Similarly, Zipkin et al. (2021) confront the issue of combining data collected at different scales. Large spatial scale research that seeks to combine disparate datasets is especially subject to such challenges. Researchers can address these concerns by considering the objectives of the work and the measurements or observations collected, using appropriate statistical approaches, and diagnosing the fundamental attributes of nonstationarity in ecological studies. Finally, researchers involved in macrosystems projects will require a wide range of specialized technical and collaborative skills, given the scale of such research; Farrell et al. (2021) highlight the potential mismatch between the skills participants perceive as important and the amount of training required to be productive in large collaborative groups.

Two examples of creating funding for areas of enduring ecological research

The NSF-funded programs Dynamics of Coupled Natural and Human Systems (CNHS; note: this program name has
changed several times and is currently titled Dynamics of Integrated Socio-Environmental Systems (DISES)) and Long Term Ecological Research (LTER) are examples of funding sources and development of ecological research that could point to the future of macrosystems research. Both areas of study have received considerable financial support from the NSF over the years, spawning a substantial amount of research. The LTER program was initially funded in the early 1980s, and funding continues to this day, with some site turnover. This program has trained generations of scientists, produced influential and insightful publications, created a network of ecological research sites across the continent (and related sites internationally), and expanded the frontiers of ecological information management. A Web of Science search (conducted June 2019) using the exact term “long term ecological research” yielded 1100 papers, with the earliest published in 1983. The number of publications peaked at 84 in 2016, and papers have received an average of 32.7 citations.

Did either of these NSF initiatives create an independent field of study? Figure 3 suggests they did indeed. Two of the broad spatial-scale projects discussed in the text, LINX and LIDET, originated as LTER synthesis groups. Macrosystems biology may develop in a similar fashion; LaRue et al. (2021) suggest that formation of a cohesive subdiscipline has already begun, although it is too early to use citation analysis as a means of evaluating progress.

The future of macrosystems biology

Macrosystems biology or similar approaches will continue to be relevant to ecological science because small-scale methodologies do not typically upscale readily and therefore fail to adequately capture or describe large-scale spatial patterns. For example, small-scale approaches do not capture properties such as teleconnections (see Tromboni et al. 2021), and mesoscale C flux can be difficult to connect to larger scale approaches (see Ballantyne et al. 2021). Macrosystems biology offers a distinctive approach that could provide valuable ecological understanding in much the same way that long-term approaches uncovered “ecological surprises” (Dodds et al. 2012).

The big data approaches often inherent to macrosystems biology research are not without criticism. Lindenmayer and
Likens (2018) argued that starting with big data runs counter to the traditional methods of ecological research based on rigorous experimentation. While this is a valid criticism of potential problems with large-scale Earth observation networks (e.g., NEON, AmeriFlux), there are many ways to conduct scientific research, and approaches can vary across spatial scales. Large-scale science can be productive by unearthing patterns only detectable at that scale, then turning to smaller experimental studies to establish mechanisms to explain large-scale patterns. Alternatively, macrosystems approaches can be used to repeat the same experiment across a broadly distributed network of sites, leading to valuable insights based on up-scaling models (LINX collaborators 2014). Detecting macrosystems patterns via such experiments remains challenging, but large-scale observation is necessary to view the results of those experiments in their proper context.

We expect macrosystems biology will continue to grow due to the following factors. First, advancements in data collection methods and analytical capability, including remote sensing and growth in large-scale ecological data collection networks, will increase the availability and accessibility of large-scale data. This creates new opportunities for macrosystems biology research to provide broad ecological insights. Second, enhanced computational power, including high-throughput computing resources and improved computational tools like machine learning and artificial intelligence, are making large-scale analyses and modeling more feasible and affordable (McCallen et al. 2019). Finally, spatial and large-scale statistical approaches are developing rapidly in an open-source-code computing environment. Given these technological advancements, we predict that macrosystems biology research will continue to contribute to the understanding of key ecological questions, and will grow in scientific value and impact over the coming years.

Despite this promising future, many challenges await. First, more interdisciplinary integration and cross-system transdisciplinary approaches are needed. Expansion in this area will require coordinated experimental and observational approaches (Benedetti-Cecchi et al. 2018). Moreover, the success of cross-system inter- and transdisciplinary approaches depends on the ability of researchers from diverse scientific disciplines to communicate and work together effectively. Second, further technological and computational advancements will allow such key issues as data acquisition and integration, nonstationarities and scaling, and novel statistical tools and models to be addressed (see Rollinson et al. 2021). Third, macrosystems biology will grow and thrive only if it enables scientists to develop new ways to predict ecological patterns and processes. Identifying underlying theories or general principles that explain the emergence of complex properties in macrosystems will greatly advance the field. Ultimately, however, the relevance of macrosystems biology will depend on whether it provides solutions to real-world problems (e.g., disease forecasts) and translates scientific knowledge to management operations (e.g., preparation for extreme events and sustainability). Fourth, macrosystems biologists should employ traditional sources of information and integrate conventional ecological knowledge in ways that enrich local and broader scale understanding; for example, natural history can inform patterns and processes at very large scales. In addition, other approaches, such as paleoecology and multidecadal datasets (e.g., LTER data), can provide context at macroscales. Finally, training the next generation of macrosystems scientists will require a retooling and development of scientists’ skillsets, with a focus on training in interpersonal connections, project management, and project integration (see Farrell et al. 2021).

## Conclusions

The articles in this Special Issue present several aspects of macrosystems biology and its potential future as an ecological subdiscipline. As with most types of ecological research, macrosystems biology is highly integrated with many fields in ecology and other disciplines (e.g., LaRue et al. 2021). However, the recent rapid growth in research productivity (Figure 3) and the scientific and social impacts of insights generated by macrosystems biology research illustrated in this Special Issue demonstrate its potential. The emphasis on large-scale ecological problems requires ecologists to confront scale-related issues. Translating small-scale results from individual subsystems to larger scales is central to the potential success of macrosystems biology. Moreover, macrosystems biology represents a potentially transformative perspective to research because it approaches scientific questions across areas of specialization and integrates new technology. The future of macrosystems biology therefore appears promising in terms of the contributions that it can make to the broader field of ecology.

## Acknowledgements

Publication of this Special Issue was funded by the US National Science Foundation (NSF award number DEB 1928375). We thank K Weathers and members of the 2018 Macrosystems Biology PI meeting for ideas presented in this paper. EA LaRue provided helpful comments; M Binford kindly provided data on NSF Macrosystems Biology funding; and T Crowl provided information about the initial formation of the NSF Macrosystems Biology program. We acknowledge support from NSF MSB grants 1818519 and 1638704 to KCR, MSB Grant 1442562 to SC, MSB grant 1442544 to WKD, and MSB grant 1638702 to SF for funding support.

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