

The evolution of macrosystems biology

Elizabeth A LaRue^{1*}, Jason Rohr², Jonathan Knott^{1†}, Walter K Dodds³, Kyla M Dahlin⁴, James H Thorp⁵, Jeremy S Johnson⁶, Mayra I Rodríguez González¹, Brady S Hardiman^{1,7}, Michael Keller¹, Robert T Fahey⁸, Jeff W Atkins⁹, Flavia Tromboni¹⁰, Michael D SanClements^{11,12}, Geoffrey Parker¹³, Jianguo Liu¹⁴, and Songlin Fei¹

In an era of unprecedented human impacts on the planet, macrosystems biology (MSB) was developed to understand ecological patterns and processes within and across spatial and temporal scales. We used machine-learning and qualitative literature review approaches to evaluate the thematic composition of MSB from articles published since the 2010 creation of the US National Science Foundation's MSB Program. The machine-learning analyses revealed that MSB articles studied scale and human components similarly to six ecology subdisciplines, indicating that MSB has deep ecological roots. A comparison with 84,841 ecological studies demonstrated that MSB has extended the knowledge space of ecology by examining large-scale patterns and processes alongside anthropogenic factors, which was also confirmed by the qualitative literature review approach. Our analyses indicated that MSB emphasizes large scales, has deep roots in ecological disciplines, and may emerge as a new research frontier, but this last point has yet to be proven.

Front Ecol Environ 2021; 19(1): 11–19, doi:10.1002/fee.2288

Over the past several decades, ecologists have begun to recognize that individual processes, no matter how limited in scope, are connected to broader spatial and temporal scales and to the Earth system as a whole (Bonan 2008). Improvements in the resolution of Earth system modeling, the availability of remotely sensed observations, and the growth of large, complex datasets have enabled scientists to begin conducting

critically needed broad-scale ecological research (Clark *et al.* 2001; Schimel and Keller 2015). The US National Science Foundation's (NSF) Macrosystems Biology (MSB) Program (currently Macrosystems Biology and NEON-Enabled Science) was created in 2010 to help address these issues (Gholz and Blood 2016), partially because the origin and symptoms of many environmental threats are global in nature. The goal of this program was to provide funding for scientists to conduct “quantitative, interdisciplinary, systems-oriented research on biosphere processes and their complex interactions with climate, land use, and invasive species at regional to continental scales” (NSF 2018). The study of MSB was intended to employ existing and new data sources to better understand ecological processes within macrosystems and to address large global challenges caused by anthropogenic impacts (Figure 1; Schimel and Keller 2015).

Shortly after the creation of the NSF MSB Program, MSB was defined as systems having biological, geophysical, and social components (Table 1). The study of MSB is also described as a hierarchical approach for understanding how spatial or temporal levels within a higher-level region to continent focal level (ie macrosystem) influence ecological processes at other levels (Figure 2; Heffernan *et al.* 2014). We refer to scale as the spatial or temporal extent of a level within or of the macrosystem itself, and a level is the spatial or temporal extents of different components within the macrosystem hierarchy. Since the creation of the NSF MSB Program in 2010, 273 projects have been funded, suggesting that this new discipline should be beginning to make a contribution to the understanding of broad-scale ecology. For example, MSB studies have developed new methods to analyze broad-scale data (eg Hamil *et al.* 2016) and new theories of ecological principles at broad spatial scales (eg Walter *et al.* 2018).

MSB builds upon theories from ecological scaling, hierarchy, and social-ecological systems (Rose *et al.* 2017),

In a nutshell:

- Macrosystems biology (MSB) was designed to study the biological, geophysical, and social components of ecological systems across temporal and regional to continental scales, but no quantitative study has evaluated its themes and place in ecology relative to other subdisciplines that focus on broad scales
- Using machine learning in automated content analysis and qualitative literature review approaches, we studied MSB literature, six closely related ecological subdisciplines, and major ecology journals published in the past four decades
- MSB has deep roots in ecological subdisciplines that focus on broad scales, while addressing novel large-scale issues and considering anthropogenic factors

¹Department of Forestry and Natural Resources, Purdue University, West Lafayette, IN (*elarue@purdue.edu); †current address: Department of Integrative Biology, Michigan State University, East Lansing, MI;

²Department of Biological Sciences, University of Notre Dame, Notre Dame, IN; ³Division of Biology, Kansas State University, Manhattan, KS; ⁴Department of Geography, Environment, and Spatial Sciences and Program in Ecology, Evolutionary Biology, and Behavior, Michigan State University, East Lansing, MI; ⁵Kansas Biological Survey and Department of Ecology and Evolutionary Biology, University of Kansas, Lawrence, KS; ⁶Department of Environmental Studies, Prescott College, Prescott, AZ; (continued on last page)



Figure 1. Macrosystems biology (MSB) is aimed at combating global-scale anthropogenic threats, such as (a) climate change (global projected change of historical precipitation to 2021–2040); (b) land-use change, represented by this rural farm in Ethiopia; and (c) biological invasions, for example by the spotted lanternfly (*Lycorma delicatula*), which is native to Asia but has spread to the US.

inevitably sharing similarities with its disciplinary predecessors (Beck *et al.* 2012; Fei *et al.* 2016). However, it is unknown how MSB has developed from its beginning to address large-scale ecological problems. It is useful to understand the large-scale and ecological themes that MSB is exploring and how it compares to other disciplines in ecology, but there are no quantitative analyses that provide such a snapshot of the MSB literature. A quantitative literature analysis of MSB would aid scientists in understanding how MSB studies are collectively addressing the types of questions that the NSF MSB Program and early definitions intended, and how MSB overlaps with closely related disciplines that also address broad-scale problems in ecology. To investigate this topic, we used automated content analysis (ACA) to provide a current snapshot of the ecological themes studied by MSB and its use of large-scale approaches in relation to similar subdisciplines. ACA is an

increasingly popular quantitative tool for big literature analysis (Nunez-Mir *et al.* 2016), as it can be used to rapidly identify and quantify common themes in, and compare the thematic content of, different bodies of literature. Specifically, we evaluated the following questions with ACA: first, what themes have MSB studies been looking at since the NSF MSB Program was introduced? Second, how similar are MSB studies to themes published in the ecological literature? And third, how do MSB studies compare to the published literature of other broad-scale disciplines in their use of spatial and temporal extents, cross-scale approaches, and the human dimension? We then discuss the future niche of MSB in the context of these results.

Thematic content of MSB within the context of broad-scale ecological disciplines

Literature analyzed and ACA methods

We conducted an analysis of MSB peer-reviewed literature to characterize themes found within abstracts published from 2010–2018 and to compare how scaling extents and consideration of the human dimension corresponded to other disciplines (Table 1). To locate published MSB literature, we conducted keyword searches on Web of Science using the keywords listed in Fei *et al.* (2016); these consisted of “macrosystems ecology”, “macrosystems biology”, “macroecology”, and “macrosystems”. We also extracted published articles from final reports of projects funded through the NSF MSB Program and used the award ID of these grants to search Web of Science for any additional articles published beyond their funding terms. In total, we collected abstracts and titles from 1788 published MSB studies. Because MSB is a relatively new area of study, there are not yet any journals devoted solely to MSB research and few authors are identifying their publications as MSB. Therefore, this literature search provided a representative sample of the MSB literature with an emphasis on studies published as a result of the NSF MSB Program.

ACA to identify concept themes within MSB studies

We used ACA to identify common themes throughout the published MSB literature. We used the text-mining program Leximancer (V4; 100 Leximancer Pty Ltd; Brisbane, Australia), which exploits text parsing and machine learning to identify the main topics in a body of text (Smith and Humphreys 2006; Nunez-Mir *et al.* 2016). We followed the method described by McCallen *et al.* (2019) to identify common concepts in the literature and to group these concepts into MSB concept themes. Briefly, we used Leximancer to identify commonly occurring concept seeds (commonly occurring words) within the 1788 MSB abstracts and afterward manually removed uninformative words from the English language or to

Table 1. Definitions of macrosystems biology (MSB) and related subdisciplines that address ecological questions at broad scales and the main grand challenges described for each discipline (WebTable 4)

Discipline	Definition	Grand challenges and key issues				
		Human ecological impacts	Scaling and connectivity	Biodiversity and ecosystem function	Human health and services	Methods, forecasting, and data
Macrosystems biology	Treats the components of regions to continents as a set of interacting parts of a system (Heffernan <i>et al.</i> 2014)					
Landscape ecology	Spatial variation in landscapes at different scales (IALE 2018)					
Geography	Study of places and the relationships between people and their environments					
Earth system science	The current picture of our planet as a whole, including its changing climate (NASA 2003)					
Ecology	The study of the relation of organisms or groups of organisms to their environment (Odum 1959)					
Biogeography	Documents and understands spatial patterns of biodiversity (Blackburn and Gaston 2002)					
Ecosystem ecology	Organisms interacting with the environment that leads to a flow of energy causing defined trophic structure, biotic diversity, and material cycles (Weathers <i>et al.</i> 2016)					

science. An iterative bootstrapping algorithm within Leximancer was used to build a definition for each concept based on commonly co-occurring words; Leximancer then counted the number of text segments containing each concept to provide a co-occurrence matrix of concepts (Alexa and Zuell 2000). To identify groups of closely related concepts, we followed an iterative approach of clustering the concept co-occurrence matrix and removing concepts that included principles of experimental design, proper nouns, locations, and organisms below the family level. A total of 315 concepts clustered into 23 themes were ultimately identified (more details about the methods used are presented in WebTable 1).

MSB studies within ecological concept space

McCallen *et al.* (2019) identified the top 46 ecology themes from four decades of literature published in the top 33 ecological journals by impact factor, and we compared the relatedness of MSB studies to these 46 themes in an ACA. We used Leximancer to analyze the frequency of the 46 compound concepts described by McCallen *et al.* (2019) in 1788 MSB abstracts and 84,841 abstracts from 33 ecology journals. We compared the proximity of MSB studies in relation to the 46 thematic groups within the ecological literature based on the first two axes of a principal coordinates analysis (PCoA).

ACA for spatial and temporal extents and the human dimension

We conducted a hand-seeded ACA with Leximancer (eg Nunez-Mir *et al.* 2015) to measure the frequency of studies that included indicators of analysis at different spatial and temporal extents, cross-scale approaches, and the human dimension. We focused on differences in the spatial and temporal extents between MSB and related disciplines and their cross-scale approaches, because large scale and cross-scale approaches are clearly defined as specific and potentially novel aspects of MSB (see WebTable 2 for terms indicative of extents). We also compared terms among bodies of literature from each discipline indicative of human-related research in a separate analysis (WebTable 2). An inherent assumption of ACA analyses is that concepts are used similarly across different bodies of literature, and as such there is potential for shifts in concept meanings across subdisciplines. Therefore, to improve the robustness of our analysis for interdisciplinary comparisons, we merged similar concepts into compound concepts (WebTable 2). We used Scopus to download titles and abstracts from articles published from 2010–2018 in journals representative of six broad-scale disciplines: geography, ecology, Earth system science, biogeography, landscape ecology, and ecosystem ecology. Journals were chosen based on their 5-year impact factor (WebTable 3) to avoid author bias in the

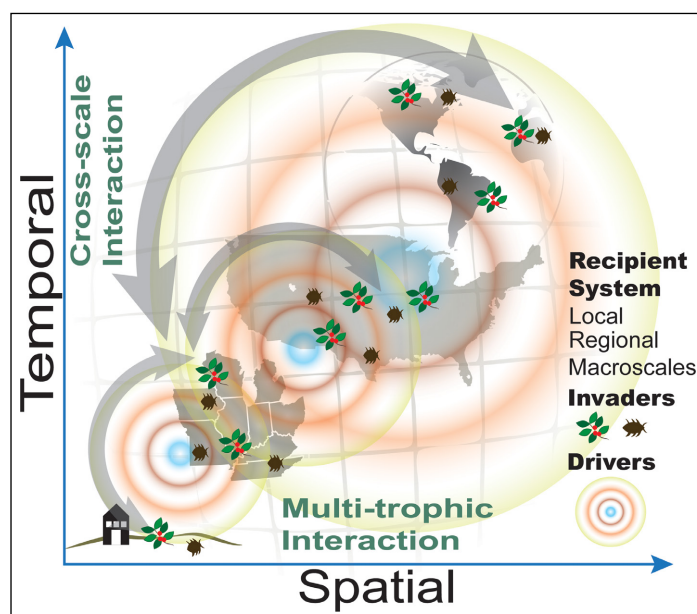


Figure 2. The biological invasion macrosystem; the movement of invasive species across regions and continents to recipient systems can cause cross-scale and multitrophic interactions across spatial and temporal scales.

choice of journals representing each discipline (ie emphasizing journals in disciplines in which their articles are most heavily cited).

We searched for words related to temporal and spatial extents or the human dimension with a hand-seeded ACA to calculate how often studies used a cross-scale (ie hierarchical) approach where two or more spatial or temporal scales co-occur. First, we searched for the scale extents and human dimensions across all journals and in each subdiscipline in Leximancer. We tested for subdisciplinary clusters that varied

by scale extents and human dimensions with a Ward's variance clustering method (Bray and Curtis 1957). The number of clusters was defined by the highest cophenetic correlation value (Sokal and Rohlf 1962). Second, we calculated the co-occurrence of different spatial and temporal categories by dividing the number of abstracts within a journal that exhibited a cross-scale approach by the total number of abstracts flagged for at least one spatial or temporal scale, respectively. Additional methodological details are presented in WebTable 2.

Qualitative analysis of NSF MSB Program abstracts

We conducted a focused qualitative analysis on the cross-scale approaches used in MSB and the ecological problems being addressed to supplement the ACA. To do so, we manually scored the abstracts of NSF grant awards to date (August 2019) for the ecological problems being addressed and the frequency of cross-scale approaches. We compared the ecological problems being addressed by MSB to the description of the main grand challenges described as the focus for the six subdisciplines (literature search details are presented in WebTable 4). We also manually scored the cross-scale approach of spatial and temporal extents described in the abstracts of NSF grant awards and in 100 randomly selected MSB publications for a similar cross-scale analysis to the ACA. Finally, the numerical values of spatial and temporal extents for each of the 100 randomly selected MSB publications were also recorded.

MSB themes and MSB in ecological space

We identified the top 23 concept themes that have been addressed in MSB studies with ACA (Table 2). These thematic groups address many human environmental issues, which is consistent with previous studies that included the social aspect as a critical component of MSB (Liu *et al.* 2007; Thorp 2014; Rose *et al.* 2017). Many of the thematic groups also involved traditional ecological concepts and methods addressed at broad spatial scales.

We found that while MSB studies fell in close proximity to many traditional thematic groups studied in ecology over the past four decades (McCallen *et al.* 2019), MSB is also at the emerging edge of an ecological thematic space that investigates broad-scale ecology and the Anthropocene (Figure 3). Overall, we identified the first two axes of the PCoA as major contributors to the explanation of variance between 46 ecological thematic groups (Figure 3). These two axes explained 40% of the variance in the dataset, indicating substantial variation in the relationship between these 46 thematic groups and MSB. MSB was situated in the middle of PCoA axis 1. Other thematic groups situated near the center of PCoA axis 1 were disturbances, forests, and aquatic processes, indicating that MSB studies have addressed traditional ecological themes. MSB was situated at the edge of PCoA axis 2, in close proximity to anthropogenic, management and policy, geospatial, long-term trends, and climate-change thematic groups, suggesting that MSB is

Table 2. Thematic groups addressed in MSB identified by associated concepts

Theme	
Anthropogenic impacts and climate change	Microbial metabolism and genetics
Biogeochemical cycling	Modeling, statistics, networks
Carbon cycling	Paleorecords
Citizen science	Pathogens
Community processes across scales	Phenology of vegetation
Continental aquatic ecosystems	Phylogenetics
Evolution	Physiological responses to climate
Extinction threats and invasion	Remote sensing
Global forests and climate	Species distributions
Hydrologic system across space and time	Urban provisioning
Isotopic aging	Weather
Macroscale diversity and biogeography	

Notes: concepts underlying each thematic group are presented in WebTable 1.

addressing topics at one of the cutting edges of ecological research that interfaces with global and anthropogenic research.

Scale extents, the human dimension, and cross-scale approach in broad-scale disciplines

We found similarities in scale extents and the human dimension between MSB and related disciplines, as demonstrated by the overlap in spatial and temporal extents, and human dimension concepts among literature groups. We found that four clusters best illustrated the spatial and temporal extents of MSB and related disciplines (Figure 4a). When considering space and time together, MSB studies were most closely aligned with ecology, geography, and biogeography (Figure 4a). Moreover, MSB clustered with biogeography, landscape ecology, and ecosystem ecology in their frequency of the incorporation of the human dimension (Figure 4b).

We expected that MSB was likely to have greater cross-scale approaches than other sub-disciplines (ie systems approach defined by Heffernan *et al.* [2014]), but no evidence was found to support this hypothesis. The ACA analysis showed that MSB did not have a significantly greater frequency of a cross-scale approach than six broad-scale disciplines (Figure 5). However, this may not be surprising, given that large-scale studies often inherently utilize local-scale data integrated across a large spatial scale (Azaele *et al.* 2015). The qualitative analysis of the frequency of a cross-scale approach showed a slightly higher frequency for space than the ACA analysis, but not for temporal scale in the abstracts of NSF grant awards: (1) abstracts of NSF grant awards showed that the cross-scale frequency was 79.6% for space and 15.2% for time, and (2) a subset of 100 MSB articles showed a spatial cross-scale frequency of 64.9% and temporal cross-scale frequency of 39.2%.

■ What should the future of MSB look like?

While MSB researchers have studied themes in ecology at and within large scales, MSB overlapped with other broad-scale disciplines in our analysis. MSB is closely related to biogeography, ecology, and geography in its treatment of spatial and temporal extents, and with biogeography, ecosystem ecology, and landscape ecology in its use of the human dimension (Figure 4). This is not surprising given MSB's strong historical roots in ecological scaling, landscape ecology, and social-ecological systems (Rose *et al.* 2017). However, MSB

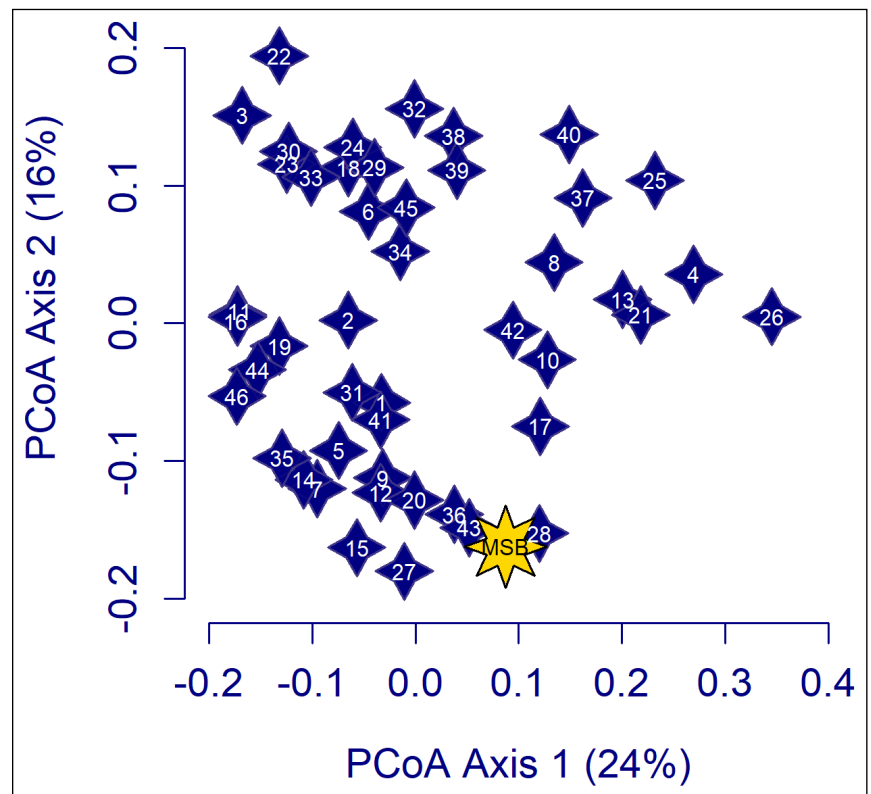


Figure 3. MSB studies in relation to 46 ecological concept themes from automated content analysis in McCallen *et al.* (2019). The yellow star represents MSB studies in relationship to the 46 ecological concept themes based on co-occurrence frequency of concepts in a principal coordinates analysis (PCoA). Numbers indicate the ecological theme: (1) modeling, (2) community processes, (3) behavior and sex, (4) biogeochemistry, (5) landscape, (6) developmental, (7) species distributions, (8) seasonal trends, (9) community structure, (10) forests, (11) genetics, (12) scales, (13) physiography, (14) paleo- and biogeography, (15) management and policy, (16) macroevolution, (17) disturbances, (18) food webs, (19) movement, (20) large scale, (21) aquatic environment, (22) life history, (23) traits, (24) survivorship, (25) plant structure and productivity, (26) gas flux, (27) anthropogenic, (28) climate change, (29) plant reproduction, (30) disease, (31) invasions, (32) cellular, (33) competition, (34) carrying capacity, (35) conservation, (36) long-term trends, (37) microbial, (38) herbivory, (39) stress, (40) plant physiology, (41) environmental patterns, (42) aquatic processes, (43) geospatial, (44) population dynamics, (45) agronomy, and (46) population demographics.

is at the emerging frontier of addressing large-scale and anthropogenic ecological questions (Table 1; Figure 3), which is consistent with previous definitions (Heffernan *et al.* 2014; Thorp 2014). This suggests that MSB is particularly important for areas where ecology intersects with human impacts and the application of ecology in the management of broad-scale systems. Indeed, MSB and all of the other subdisciplines are heavily focused on addressing the grand challenge of human environmental impacts (Table 1). Our study suggests that MSB is similar to other ecological subdisciplines that seek to address anthropogenic problems at large scales. However, many questions remain about MSB (Fei *et al.* 2016; Rose *et al.* 2017), the answers to which are needed to understand the hierarchical nature of macrosystems and anthropogenic impacts on global ecosystems. Here, we suggest several areas

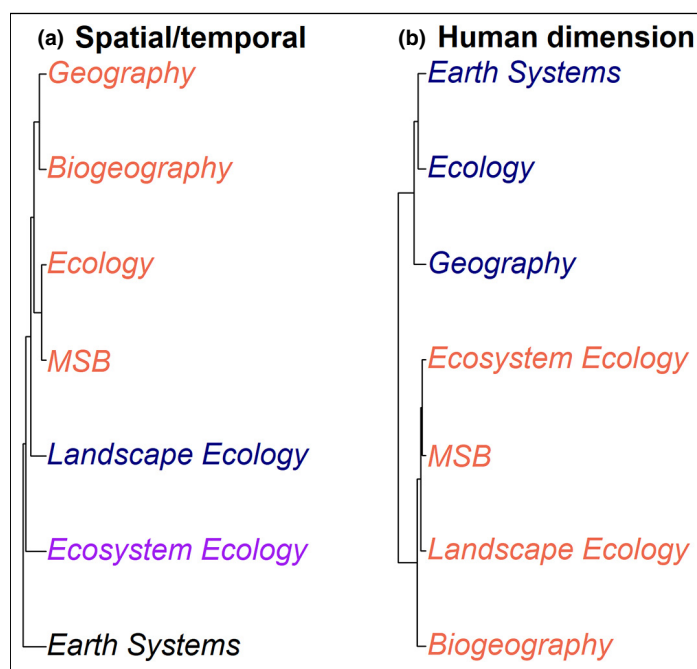


Figure 4. Scaling and human dimension clustering of MSB and journals from related ecological subdisciplines as identified from a hand-seeded automated content analysis (ACA). (a) Clustering of MSB studies with other journals across spatial and temporal spatial extents (WebTable 2). (b) Clustering of MSB studies with other journals across human dimension concepts. Clusters are indicated by different colors. Journals were combined by their respective subdiscipline. The co-occurrence matrix was row-normalized and a Bray–Curtis dissimilarity matrix was calculated prior to the clustering analysis. Representative journals for subdisciplines are listed in WebTable 3.

that could be prioritized for future MSB research to move the field forward.

Cross-scale analyses

Cross-scale analyses are critical for understanding the hierarchical nature of MSB because they influence ecological factors, such as species distributions (Cohen *et al.* 2016), community diversity (Anderson 2018), and biotic resistance (Iannone *et al.* 2016). The ACA illustrates that MSB studies do address cross-scale relationships, but do not do so substantially more or less often than other disciplines (Figure 5). The ACA is heavily based on publications from previously funded NSF MSB projects, but abstracts of NSF MSB awards had a higher spatial cross-scale frequency than published MSB studies. Cross-scale results from ongoing NSF awards may not yet be fully reflected in the literature. We also acknowledge that the National Ecological Observatory Network (NEON) and its 81 field sites have recently transitioned to full operations, providing a large suite of data aimed at advancing MSB. NEON resources will likely form the basis of a new generation of MSB studies. At the moment, however, our understanding of the hierarchical nature of macrosystems is still incomplete (Soranno *et al.* 2014), but we do know that if cross-scale relationships are ignored they can lead to contradicting conclusions at different

scales (Hamil *et al.* 2016). Our expectation is that knowledge about the cross-scale phenomenon in MSB will continue to expand in the future.

Scaling

There is a long history of research on scaling in ecology (particularly landscape ecology) in recognition of the problem that ecological phenomena that occur at one spatial extent may not hold true at another extent (Wiens 1989; Levin 1992; Schneider 2001). Ecological dynamics are more often stochastic at local scales than regional scales, but this pattern depends largely on the scale described and the ecological phenomena of interest (Chave 2013). MSB has built upon its biogeography and ecological predecessors to provide new large-scale tests of biodiversity (Heino 2011; Wilson *et al.* 2012), nutrient patterns (Elser *et al.* 2007), and classical scaling hypotheses (Soranno *et al.* 2019). Nevertheless, despite decades of scientific investigation, ecological scaling remains an active area of inquiry, with substantial uncertainty remaining about how ecological knowledge can be applied from one scale to another. It is critical to ask at what point ecological principles disappear or emerge along spatial- and temporal-scale gradients, and what are the mechanistic underpinnings causing these scaling patterns.

Bounding a macrosystem

We found that a subset of 100 MSB studies had a mean spatial extent of 55,870,409 km² (median 689,976 km²) and a time span of 766,694 years (median 8 years), indicating that MSB studies are meeting their defined focal spatial extent of region to continent (no defined time span). As with the term “community”, a precise definition of “a macrosystem” remains elusive, however (Stroud *et al.* 2015). The practical definition of a macrosystem is likely to vary with the study question and occur along a continuum of spatial and temporal extents. A macrosystems approach may not require the spatial extent of a study to occur at *macroscales* (eg hierarchical components within a microbial system; Borer *et al.* 2013). There is value in the macrosystem definition including nested spatial or temporal components within a large spatial extent, especially for addressing the unprecedented global human-caused problems. Future research could further evaluate if the presence of unique ecological phenomena occurring only at macroscales indicates whether this definition is ecologically warranted.

Solving grand challenges: human ecological impacts

Our quantitative (Table 2) and qualitative (Table 1) analyses both show that MSB has centrally focused on contemporary environmental threats, often referred to as grand challenges. Due to their frequently large spatial extent, macrosystems include both human and natural systems, which forces MSB theory to consider the human dimension (Liu 2017; Rose *et al.* 2017). The NSF MSB Program was formed in part

because many environmental problems that are caused by humans originate at a global scale. Although understanding ecology in light of the human dimension is not unique to MSB (Table 1), human-driven impacts pose such a large threat to ecological systems that the contribution of MSB in addition to many other disciplines is needed to solve these anthropogenic problems. Therefore, we re-emphasize that human (social) components of macrosystems are crucial research foci for MSB, and that funding priorities in the future should explicitly encourage such studies. For example, urban areas are an understudied type of macrosystem (Groffman *et al.* 2014; Lahr *et al.* 2018), and the flow of ecosystem services across urban macrosystems is heavily moderated by human activities (WebFigure 1).

MSB studies are aiding the search for solutions to human ecological impacts by developing open-source data networks and modeling approaches, and by describing large-scale consequences of global change. Large-scale data collection by NEON is closely intertwined with MSB and will allow scientists to test the impact of climate change on macrosystems through scaling theories, such as metacoupling (Liu 2017) and new dimensions of diversity (LaRue *et al.* 2019). Ecological forecasting is emerging as a popular approach to understanding short-term ecological impacts of human activities in MSB (Dietze 2017) and Earth systems science (WebTable 4). Furthermore, MSB is developing better modeling approaches for predicting species responses to climate change (Wisz *et al.* 2013), which are necessary for developing climate-change mitigation plans. A number of MSB studies have also described critical consequences of climate change (Cohen *et al.* 2018) and widespread diseases (Civitello *et al.* 2015). Despite these new approaches and tests of global change impacts by MSB, a mature body of empirically supported hypotheses or management approaches derived solely from MSB literature is lacking. Overall, the subdisciplinary approaches for solving the grand challenge of human ecological impacts may be unique or they may build upon each other. Future literature analysis of MSB could take an in-depth qualitative approach (eg thick descriptive) to tease apart the contributions of MSB and other ecological subdisciplines to large-scale theory and approaches to solving global change. However, the critical task is solving human ecological impacts, and MSB has been heavily invested in this effort.

Conclusion

Throughout the history of science, disciplines and concepts have been regularly reframed, which has often propelled science to important new discoveries and advances (eg eco-evolutionary dynamics as a reframed subfield of evolutionary ecology; Reznick 2013). Prior to the development of the NSF MSB Program in 2010, MSB studies existed under a broad array of headings, including Earth system

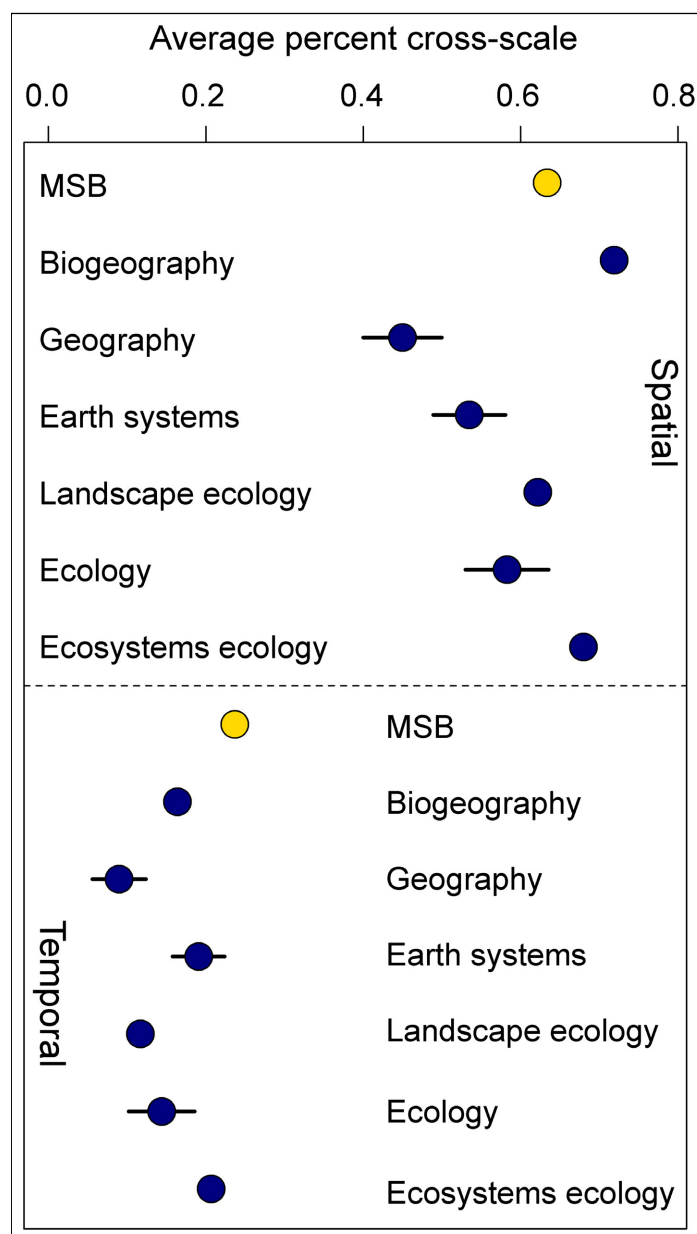


Figure 5. Percentage of spatial and temporal cross-scale approaches in ecological subdisciplines identified from hand-seeded ACA. A single value of percentage of spatial and temporal extent co-occurrence categories was calculated for each journal as the count of articles that employed a cross-scale approach out of the total count of articles that were tagged as spatial or temporal in that journal from 2010–2018. Values were averaged across representative journals (WebTable 3) from each subdiscipline when there was more than one journal, and the standard error is shown.

science, landscape ecology, and biogeography. Despite the overlap between MSB and disciplines that preceded it, this reframing of the study of large-scale biological processes should not take away from the utility of MSB or its sister disciplines. Part of the reframing that impelled the genesis of MSB was the realization that the consequences of many anthropogenic changes – such as those associated with biotic

homogenization (Groffman *et al.* 2014), exotic invasion (Iannone *et al.* 2016), and climate change (Adger *et al.* 2008) – might not manifest for decades, and could transcend biogeographic and arbitrary human boundaries spanning regions, continents, and the globe. These aspects of social-ecological systems require studies at broad spatiotemporal scales. If science focuses on short temporal and small spatial scales simply because they are logistically easier to study, it will inevitably produce an incomplete understanding of some of the consequences of anthropogenic change and may miss potential solutions to the most pressing environmental problems. Thus, MSB could be a particularly relevant discipline in predicting and mitigating future catastrophes associated with the Anthropocene. We expect that MSB will offer vital scientific advances to society at the forefront of global change.

Acknowledgements

Publication of this Special Issue was funded by the US National Science Foundation (NSF award number DEB 1928375). The idea for this article resulted from a series of conversations that began at the NSF's Macrosystems Biology meeting in Alexandria, Virginia, in January 2018. K Rose provided early feedback and travel support to EAL through NSF 1818519; EAL was also supported in part by NSF 1638702 to SF and BSH; JL was supported by NSF 1340812, NSF 1518518, and Michigan AgBioResearch; KMD was funded in part by NSF 1702379; FT was funded by NSF 1442562; JSJ was supported by NSF 1340852; and JWA was supported by NSF 1655095. Author contributions: EAL and SF came up with the initial idea and the other authors contributed to further study conceptualization; EAL, JK, MK, and KMD conducted the analyses; EAL, JR, JSJ, and WKD wrote the initial draft; and all authors contributed to editing.

References

- Adger WN, Eakin H, and Winkels A. 2008. Nested and teleconnected vulnerabilities to environmental change. *Front Ecol Environ* **7**: 150–57.
- Alexa M and Zuell C. 2000. Text analysis software: commonalities, differences and limitations: the results of a review. *Qual Quant* **34**: 299–321.
- Anderson CB. 2018. Biodiversity monitoring, Earth observations and the ecology of scale. *Ecol Lett* **21**: 1572–85.
- Azaele S, Maritan A, Cornell SJ, *et al.* 2015. Towards a unified descriptive theory for spatial ecology: predicting biodiversity patterns across spatial scales. *Methods Ecol Evol* **6**: 324–32.
- Beck J, Ballesteros-Mejia L, Buchmann CM, *et al.* 2012. What's on the horizon for macroecology? *Ecography* **35**: 673–83.
- Blackburn TM and Gaston KJ. 2002. Macroecology is distinct from biogeography. *Nature* **418**: 723–23.
- Bonan GB. 2008. Forests and climate change: forcings, feedbacks, and the climate benefits of forests. *Science* **320**: 1444–49.
- Borer ET, Kinkel LL, May G, *et al.* 2013. The world within: quantifying the determinants and outcomes of a host's microbiome. *Basic Appl Ecol* **14**: 533–39.
- Bray JR and Curtis JT. 1957. An ordination of the upland forest communities of southern Wisconsin. *Ecol Monogr* **27**: 325–49.
- Chave J. 2013. The problem of pattern and scale in ecology: what have we learned in 20 years? *Ecol Lett* **16**: 4–16.
- Civitello DJ, Cohen J, Fatima H, *et al.* 2015. Biodiversity inhibits parasites: broad evidence for the dilution effect. *P Natl Acad Sci USA* **112**: 8667–71.
- Clark JS, Carpenter SR, Barber M, *et al.* 2001. Ecological forecasts: an emerging imperative. *Science* **293**: 657–60.
- Cohen JM, Civitello DJ, Brace AJ, *et al.* 2016. Spatial scale modulates the strength of ecological processes driving disease distributions. *P Natl Acad Sci USA* **113**: E3359–64.
- Cohen JM, Lajeunesse MJ, and Rohr JR. 2018. A global synthesis of animal phenological responses to climate change. *Nat Clim Change* **8**: 224–28.
- Dietze MC. 2017. Ecological forecasting. Princeton, NJ: Princeton University Press.
- Elser JJ, Bracken MES, Cleland EE, *et al.* 2007. Global analysis of nitrogen and phosphorus limitation of primary producers in freshwater, marine and terrestrial ecosystems. *Ecol Lett* **10**: 1135–42.
- Fei SL, Guo QF, and Potter K. 2016. Macrosystems ecology: novel methods and new understanding of multi-scale patterns and processes. *Landscape Ecol* **31**: 1–6.
- Gholz HL and Blood ER. 2016. MacroSystems Biology: stimulating new perspectives on scaling in ecology. *Landscape Ecol* **31**: 215–16.
- Groffman PM, Cavender-Bares J, Bettez ND, *et al.* 2014. Ecological homogenization of urban USA. *Front Ecol Environ* **12**: 74–81.
- Hamil KD, Iannone BV, Huang WK, *et al.* 2016. Cross-scale contradictions in ecological relationships. *Landscape Ecol* **31**: 7–18.
- Heffernan JB, Soranno PA, Angilletta MJ, *et al.* 2014. Macrosystems ecology: understanding ecological patterns and processes at continental scales. *Front Ecol Environ* **12**: 5–14.
- Heino J. 2011. A macroecological perspective of diversity patterns in the freshwater realm. *Freshwater Biol* **56**: 1703–22.
- IALE (International Association for Landscape Ecology). 2018. What is landscape ecology? www.landscape-ecology.org/about-iale/what-is-landscape-ecology.html. Viewed 31 Mar 2020.
- Iannone BV, Potter KM, Hamil KD, *et al.* 2016. Evidence of biotic resistance to invasions in forests of the eastern USA. *Landscape Ecol* **61**: 85–99.
- Lahr EC, Dunn RR, and Frank SD. 2018. Getting ahead of the curve: cities as surrogates for global change. *P Roy Soc B-Biol Sci* **285**: 1–9.
- LaRue EA, Hardiman BS, Elliott JM, and Fei S. 2019. Structural diversity as a predictor of ecosystem function. *Environ Res Lett* **14**: 114011.
- Levin S. 1992. The problem of pattern and scale in ecology: The Robert H MacArthur Award Lecture. *Ecology* **73**: 1943–67.
- Liu J, Dietz T, Carpenter SR, *et al.* 2007. Complexity of coupled human and natural systems. *Science* **317**: 1513–16.
- Liu J. 2017. Integration across a metacoupled world. *Ecol Soc* **22**: 29.
- McCallen E, Knott J, Nunez-Mir G, *et al.* 2019. Trends in ecology: shifts of ecological research themes in the last four decades. *Front Ecol Environ* **17**: 109–16.

- NASA (National Aeronautics and Space Administration). 2003. 2003–05 Earth Science Enterprise Division Plans. Washington, DC: NASA.
- NSF (National Science Foundation). 2018. Macrosystems Biology Program. www.nsf.gov/funding/pgm_summ.jsp?pims_id=503425. Viewed 30 Nov 2018.
- Nunez-Mir GC, Iannone BV, Curtis K, *et al.* 2015. Evaluating the evolution of forest restoration research in a changing world: a “big literature” review. *New Forest* **46**: 669–82.
- Nunez-Mir GC, Iannone BV, Pijanowski BC, *et al.* 2016. Automated content analysis: addressing the big literature challenge in ecology and evolution. *Methods Ecol Evol* **7**: 1262–72.
- Odum EP. 1959. The fundamentals of ecology. Philadelphia, PA: WB Saunders.
- Reznick DN. 2013. A critical look at reciprocity in ecology and evolution: introduction to the symposium. *Am Nat* **181**: S1–8.
- Rose KC, Graves RA, Hansen WD, *et al.* 2017. Historical foundations and future directions in macrosystems ecology. *Ecol Lett* **20**: 147–57.
- Schimel D and Keller M. 2015. Big questions, big science: meeting the challenges of global ecology. *Oecologia* **177**: 925–34.
- Schneider DC. 2001. The rise of the concept of scale in ecology: the concept of scale is evolving from verbal expression to quantitative expression. *BioScience* **51**: 545–53.
- Smith AE and Humphreys MS. 2006. Evaluation of unsupervised semantic mapping of natural language with Leximancer concept mapping. *Behav Res Methods* **38**: 262–79.
- Sokal RR and Rohlf FJ. 1962. The comparison of dendrograms by objective methods. *Taxon* **11**: 33–40.
- Soranno PA, Cheruvilil KS, Bissell EG, *et al.* 2014. Cross-scale interactions: quantifying multiscaled cause–effect relationships in macrosystems. *Front Ecol Environ* **12**: 65–73.
- Soranno PA, Wagner T, Collins SM, *et al.* 2019. Spatial and temporal variation of ecosystem properties at macroscales. *Ecol Lett* **22**: 1587–98.
- Stroud JT, Bush MR, Ladd MC, *et al.* 2015. Is a community still a community? Reviewing definitions of key terms in community ecology. *Ecol Evol* **5**: 4757–65.
- Thorp JH. 2014. Metamorphosis in river ecology: from reaches to macrosystems. *Freshwater Biol* **59**: 200–10.
- Walter JA, Sheppard LW, Anderson TL, *et al.* 2018. The geography of spatial synchrony. *Ecol Lett* **21**: 1453–53.
- Weathers KC, Groffman PM, Van Dolah E, *et al.* 2016. Frontiers in ecosystem ecology from a community perspective: the future is boundless and bright. *Ecosystems* **19**: 753–70.
- Wiens J. 1989. Spatial scaling in ecology. *Funct Ecol* **3**: 753–70.
- Wilson BJ, Peet RK, Dengler J, *et al.* 2012. Plant species richness: the world records. *J Veg Sci* **23**: 796–802.
- Wisz MS, Pottier J, Kissling WD, *et al.* 2013. The role of biotic interactions in shaping distributions and realized assemblages of species: implications for species distribution modelling. *Biol Rev* **88**: 15–30.

This is an open access article under the terms of the Creative Commons Attribution-NonCommercial-NoDerivs License, which permits use and distribution in any medium, provided the original work is properly cited, the use is non-commercial and no modifications or adaptations are made.

Supporting Information

Additional, web-only material may be found in the online version of this article at <http://onlinelibrary.wiley.com/doi/10.1002/fee.2288/supinfo>

⁷Department of Ecological and Environmental Engineering, Purdue University, West Lafayette, IN; ⁸Department of Natural Resources and the Environment and Center for Environmental Sciences and Engineering, University of Connecticut, Storrs, CT; ⁹Department of Biology, Virginia Commonwealth University, Richmond, VA; ¹⁰Global Water Center and Department of Biology, University of Nevada–Reno, Reno, NV; ¹¹The National Ecological Observatory Network, Battelle Inc, Boulder, CO; ¹²Institute of Arctic and Alpine Research, University of Colorado–Boulder, Boulder, CO; ¹³Smithsonian Environmental Research Center, Edgewater, MD; ¹⁴Center for Systems Integration and Sustainability, Department of Fisheries and Wildlife, Michigan State University, East Lansing, MI



Interested in making
a broad impact?

Don't forget
that
Frontiers
offers an
open access
option!