Cross-scale interactions: quantifying multi-scaled cause–effect relationships in macrosystems

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Ecologists are increasingly discovering that ecological processes are made up of components that are multi-scaled in space and time. Some of the most complex of these processes are cross-scale interactions (CSIs), which occur when components interact across scales. When undetected, such interactions may cause errors in extrapolation from one region to another. CSIs, particularly those that include a regional scaled component, have not been systematically investigated or even reported because of the challenges of acquiring data at sufficiently broad spatial extents. We present an approach for quantifying CSIs and apply it to a case study investigating one such interaction, between local and regional scaled land-use drivers of lake phosphorus. Ultimately, our approach for investigating CSIs can serve as a basis for efforts to understand a wide variety of multi-scaled problems such as climate change, land-use/land-cover change, and invasive species.

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Many environmental problems cannot be adequately addressed by viewing them through a single lens, be it narrow or broad, because ecological interactions often cross boundaries of scale or levels of organization (Peters *et al.* 2011). Cross-scale interactions (CSIs) occur when driver and response variables in cause–effect relationships operate at different characteristic spatial and temporal scales, sometimes producing nonlinear patterns and dynamics (Carpenter and Turner 2000; Gunderson and Holling 2002; Peters *et al.* 2007). Understanding these relationships is necessary to predict likely outcomes of alternative management strategies intended to mitigate complex environmental problems (Miller *et al.* 2004; Peters *et al.* 2004; Tranvik *et al.* 2009). Because practitioners of macrosystems ecology study such multi-scaled interactions (Heffernan *et al.* 2014), this relatively new subdiscipline of ecology includes the study of CSIs.

In a nutshell:

- To address many pressing environmental problems, scientists need to study cause–effect relationships at both fine and broad scales across time and space
- Driver variables that control ecological processes can interact across scales, but large amounts of data collected from many regions are needed to study the processes at broad scales
- We offer an approach for measuring these types of interactions using 2100 lakes in 35 regions in North America
- This approach can be used to measure interactions across scales for other systems, to study a range of research questions

Macrosystems are made up of biological, geophysical, and sociocultural components that exhibit variation at the scale of regions to continents (Heffernan *et al.* 2014). For simplicity, we use the term "macrosystems" here to include three dominant spatial "scales" (interpreted as spatial extents, but which can be interchanged with temporal extents), and we depict the potential interactions that make up a macrosystem as arrayed along a gradient of complexity (Figure 1). Unidirectional interactions from a broader- to a finer-scaled driver or explanatory variable (green and orange arrows in Figure 1, a–d) and interactions that are bidirectional between two variables within a scale (black arrows in Figure 1, a–d) are perhaps the two most studied interaction types.

There are a growing number of examples in the literature describing the more complex relationships that occur when driver variables interact *across* scales (blue and red arrows in Figure 1, c and d). The first type of CSI occurs when there is an interaction among *driver* variables at different spatial scales that influences a focal response variable (Figure 1c; the CSI is depicted as a one-way arrow from the interaction between the driver variables to the focal response variable). For instance, consider a case in which a broad-scale regional driver such as anthropogenic disturbance affects the degree to which a local driver variable influences a focal response variable (eg Peters *et al.* 2007). Later sections of this paper present a case study documenting this type of CSI between regional agriculture and wetland patches connected to and affecting nutrient concentrations in a downstream

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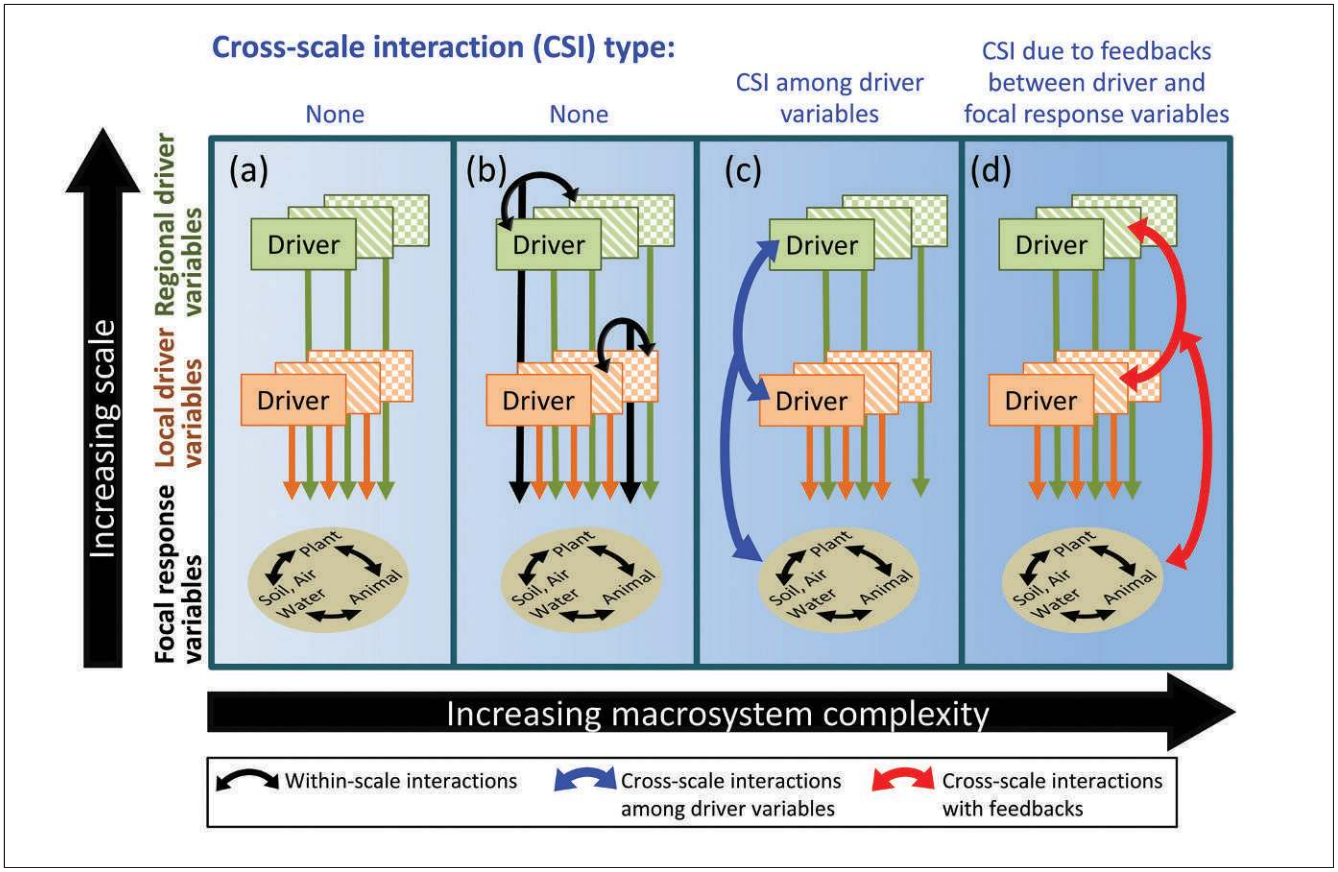

Figure 1. *A description of four types of cause–effect relationships between driver variables and response variables within macrosystems, ranging from the simplest (a), to the more complex (c and d), in which there are cross-scale interactions (CSIs). For simplicity, we depict three main spatial extents of a macrosystem: the "focal response variables" are the fine-scale processes that ecologists typically study, the "local driver variables" (orange boxes) are the variables that are measured at a coarser scale and that influence the focal response variables, and finally the "regional driver variables" (green boxes) are measured at macroscales (sub-continental to continental scales in the range of 100s to 1000s of kilometers; Heffernan* et al. *2014). The green and orange arrows depict the one-way effect of regional and local driver variables, respectively, on the focal response variable. We define "driver" variable in the most general case as any explanatory variable measured at any scale that directly influences a focal response variable. Real macrosystems can include additional extents that may exhibit a combination of different interaction types influencing the focal response variables. Some components of the figure are modified from Peters* et al. *(2008).*

lake. Other examples include tropical forest gastropod diversity being influenced by the interaction between broad-scale hurricane-induced disturbance and fine-scale historical land use (Willig *et al.* 2007), and the interactions between broad-scale forest fragmentation and local-scaled habitat variables that prevent some Chilean bird species from responding to local features that are known to affect bird abundance (Vergara and Armesto 2009).

A second type of CSI is defined by interactions between transport processes that link fine- and broad-scaled processes as described in Peters *et al.* (2007). This CSI is depicted in Figure 1d as a two-way arrow between the CSI among driver variables and the feedback from the focal response variable (referred to as cross-scale emergence in Heffernan *et al.* [2014]). For example, this type of CSI occurs when fire within patches interacts with regional heterogeneity and connectivity among forest patches to influence fire spread at broad scales, and even the climate system in the case of a very large fire (Peters *et al.* 2007). Other cases of this kind of CSI are the propagation of fine-scaled land-use effects that influence regional climate (Pielke *et al.* 2007), and patch configuration in semi-arid grazed catchments causing unexpected broad-scale sediment loss that was not equivalent to the sum of the individual finer-scaled sediment losses (Ludwig *et al.* 2007). Failure to account for the CSIs present in each of the above examples would result in a misunderstanding of the controlling factors regulating the focal response variable.

In this paper, we offer an approach that uses Bayesian hierarchical models to explicitly model the CSIs that are depicted in Figure 1c as an interaction term between a regional and a local driver variable. We illustrate the approach using 2100 north temperate lakes in which lake phosphorus (P) is the focal response variable, the local watershed characteristics of each lake are the local driver variables, and the characteristics of the 35 regions that the lakes are nested within are the regional driver variables. We end with a discussion of how such results can be applied in a management or policy context.

Steps to quantify CSIs among driver variables

CSIs can be quantified using this approach (Figure 2) for any macrosystem and set of multi-scaled drivers with the following minimum requirements: (1) hypotheses of the important cause–effect relationships linking multi-scaled driver variables to focal response variables in the macrosystem(s), (2) data on the focal response variables across broad spatial and/or temporal extents, and (3) data on the multi-scaled and multi-thematic driver variables of the macrosystem(s). With these components, one can test for multi-scaled relationships using appropriate models. These steps are iterative and many are not unique to the study of macrosystems or CSIs. However, for some steps, particular challenges arise that are a consequence of the multi-scaled scope of macrosystems ecology research and may require tools or approaches that have not been widely used by ecologists (eg Levy *et al.* 2014). In addition, for almost all of the steps discussed here, ecoinformatics (the use of software tools to manipulate, store, and distribute ecological data) is integrally linked in all aspects of the research, from database design and management to analytical operations, and ultimately to database documentation and sharing (Michener and Jones 2012; Rüegg *et al.* 2014).

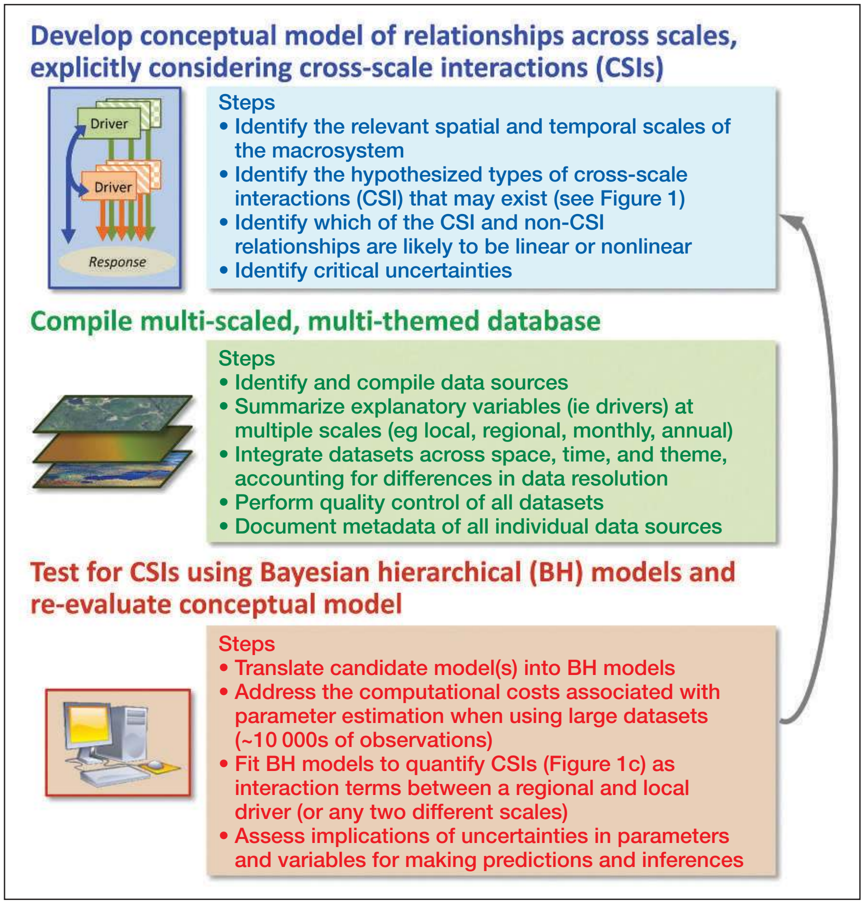

Figure 2. *The three main steps used to quantify CSIs through a multi-thematic, multi-scaled database and Bayesian hierarchical models. We focus on the compilation of especially large and spatially distributed datasets to characterize the within- and across-region heterogeneity in the study area by fitting region-varying models with sufficient data to support the models.*

Step 1: conceptual model

The first and most important step when quantifying CSIs among drivers is to translate current understanding of the macrosystem and its important multi-scaled cause–effect relationships into a conceptual model. We argue that this is one of the more challenging steps because it requires a solid working understanding of macrosystems. Four key components of conceptual model development are: (1) identifying the relevant spatial and temporal extents and resolutions of the driver variables, (2) considering what types of CSIs are expected, (3) determining whether relationships are likely to be linear or nonlinear, and (4) identifying the critical assumptions and uncertainties that may generate additional testable hypotheses (Figure 2). Our approach to quantifying CSIs is iterative. The cause–effect relationships (including CSIs) identified in this first step can be refined or new cause–effect relationships can be added during subsequent iterations and as new information becomes available.

Step 2: database design and development

Rarely are there preexisting databases that span the spatial and temporal extents necessary to conduct macrosystems ecological research. Therefore, these next steps include discovering and acquiring datasets that are distributed across space and time and integrating them into a multi-scaled, multi-thematic database. When more than a handful of datasets are incorporated into a database, numerous ecoinformatics challenges may arise (Michener and Jones 2012; Rüegg *et al.* 2014). Essential steps in database development are to identify credible data sources, to perform quality-assurance and quality-control checks, and to produce detailed documentation in the form of metadata for each dataset and the final integrated database (see Rüegg *et al.* [2014] for further details).

Step 3: analytical approaches

The analytical steps begin with translating the conceptual model into a set of models that each represents competing hypotheses to be evaluated and compared (Burnham and Anderson 2002; Stow *et al.* 2009). Such models can take

Figure 3. *Images showing the different spatial extents that are relevant for multi-scaled studies of lakes, including (a) the lake and its watershed, (b) the lake network, and (c) the freshwater region. The freshwater region classification that we use in this example is Ecological Drainage Units (Higgins* et al. *2005). There are many driver variables that can be quantified at each of these important spatial extents (eg land cover, connectivity among freshwater ecosystems and groundwater, geology, soils) based on the conceptual framework of landscape limnology (Soranno* et al. *2010). Images from The National Map – Orthoimagery, US Geological Survey, http://nationalmap.gov/ortho.html.*

many forms, including process, statistical, and/or simulation. For statistical modeling, the parameter estimation and model inference can be Bayesian or non-Bayesian. We present modeling steps using Bayesian hierarchical models, which are well suited for analyzing multi-thematic and multi-scaled data (Qian *et al.* 2010) as well as data across broad spatial (and temporal) extents with variable sample sizes and associated with unbalanced sampling designs (Gelman and Hill 2007; Cressie *et al.* 2009). Hierarchical models allow model coefficients (eg slopes and intercepts) to vary by region, which provides an elegant way to measure one type of CSI (as depicted in Figure 1c) by simultaneously modeling both the local-scale variability in the response variable of interest and the variability in regional-scale coefficients. Here, we model a CSI as an interaction term between two driver variables measured at different scales (eg orange and green boxes in Figure 1c) which influences the response variable in addition to the individual effects of the two driver variables (in Figure 1c, this interaction is depicted by the blue curved arrows; see below for further details).

Once a model or model set has been developed and estimated from the data, the ecological importance of the resulting parameter estimates and/or predictions is evaluated within the context of the hypotheses, the conceptual and analytical model(s), and the degree of uncertainty in variables or parameters. In some cases, candidate models that are not computationally feasible will have to be simplified. Once all the models have been evaluated, revisions to the conceptual model can be made and additional models created and tested iteratively.

■ Case study – understanding drivers of lake nutrients at subcontinental scales

Using lakes as model ecosystems to study CSIs

We illustrate the approach described above by modeling lake P concentrations at the subcontinental scale in 35 regions, using multi-scaled driver variables to test for a hypothesized CSI. There are strong conceptual and practical reasons for focusing on lakes for macrosystems ecology research and specifically to study CSIs. First, lakes are influenced by multiple well-studied spatial extents including the watershed, the lake network, and the freshwater region (Figure 3), as well as multiple temporal extents including daily, seasonal, interannual, decadal, and centurial scales. Although the land–water boundary of lakes is less functionally distinct than originally assumed (Cole *et al.* 2002), the physical boundary of the lake shoreline does represent a shift from aquatic to non-aquatic habitats and therefore facilitates easy map-based measurements of macrosystem variables across broad spatial extents. Second, as gathering points of water and nutrients, lakes integrate the effects of hydrologic, land-use, and climatic changes at a range of spatial and temporal scales (Williamson *et al.* 2009). Third, a wealth of data and knowledge exist for lakes, including single-scaled studies that provide the possible mechanisms needed to understand how driver variables of lake nutrients may interact across scales. Fourth, a hierarchical conceptual framework, such as that found in landscape limnology, is needed to understand the complex suite of driver variables and possible CSIs that influence lake response variables, such as nutrients (Soranno *et al.* 2010). Finally, lakes and their nutrients have the advantage that reliable data, obtained by standard methods, are widely available across broad geographic and temporal extents and can be integrated into a single database.

Does a CSI between regional agriculture and local wetland cover affect lake nutrient concentrations?

In many regions of the world, an increase in the amount of agricultural land use directly around lakes (ie local scale) has been shown to increase aquatic P concentrations (Taranu and Gregory-Eaves 2008). However, the same cannot be said for the effect of local wetland cover on lake P

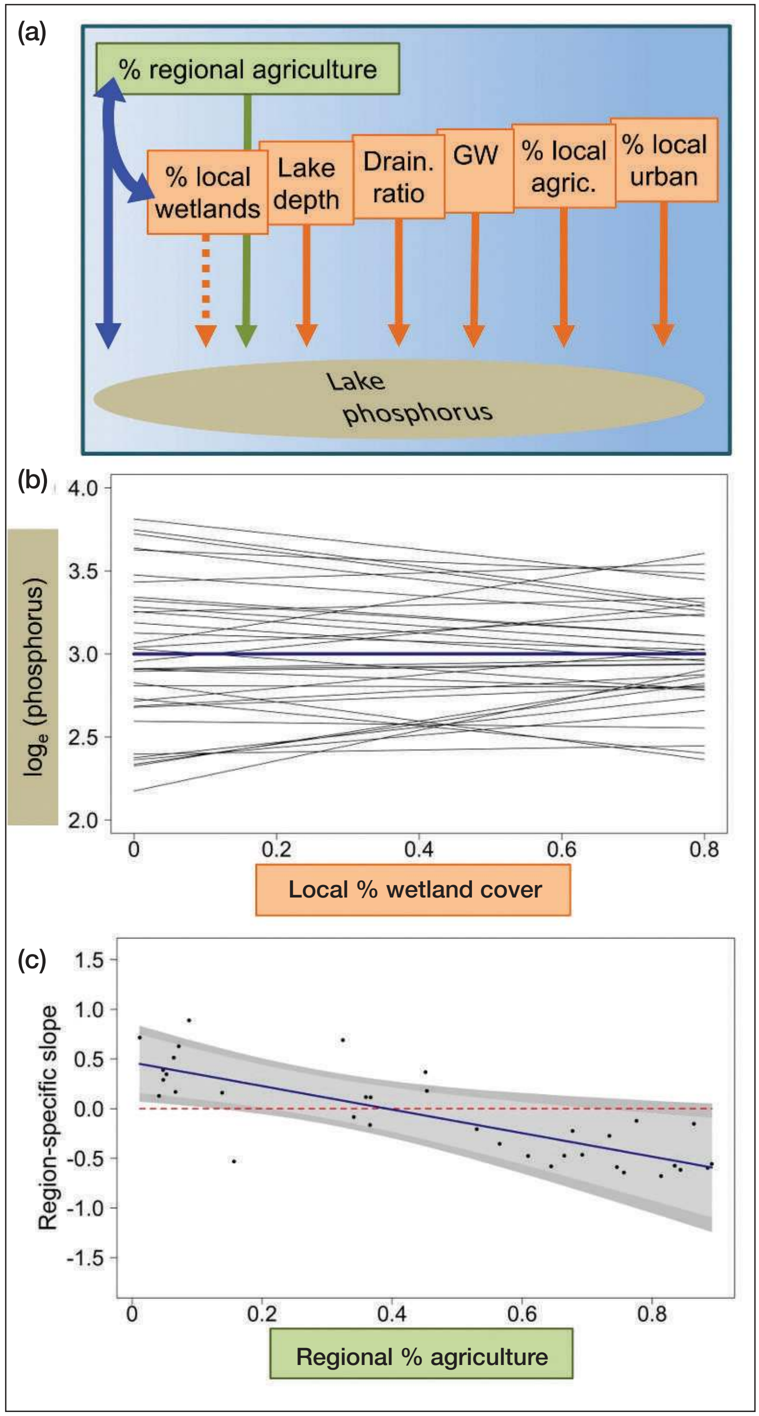

Figure 4. *The conceptual and analytical results of the case study. (a) A conceptual model of the driver variables for the Bayesian hierarchical model, in which the focal response variable is lake P; the local driver variables are: local % wetland cover around the lake, lake depth (mean depth), drainage ratio (the ratio of watershed-to-lake area), groundwater potential (measured as the % groundwater contribution to stream baseflow near the lakes), local % agriculture around the lake, and local % urban land around the lake; the CSI is an interaction term between regional % agriculture and local % wetland cover. The slope of the effect of local % wetland cover was not different from zero, so is represented by a dashed line in this conceptual figure. The model is the type of CSI depicted in Figure 1c. (b) The relationship between local % wetland cover and lake P, modeled for each region. Black lines represent region-specific relationships and the bold blue line is the population average relationship across all regions, which is not different from zero. (c) The relationship between regional % agriculture and the 35 region-specific slopes. Solid circles are region-specific slope estimates, shown with the multilevel regression line, and dark- and light-gray shaded regions are 95% and 80% credible intervals, respectively.*

concentrations. Wetland cover surrounding lakes has been found to both increase (Prepas *et al.* 2001) and decrease (Weller *et al.* 1996) the concentration of lake P, depending on the region studied. We hypothesized that these divergent relationships could be explained by a CSI, in which regional agriculture (a measure of regional anthropogenic disturbance) influences the degree to which local wetlands affect lake P concentrations. Regions dominated by agriculture also have modified hydrological, nutrient, and material connectivity that likely influence the effect that local wetlands (many of which have also been altered) have on downstream lake nutrients. Therefore, a lake in close spatial proximity to intensive agriculture (ie within its watershed boundaries), in an otherwise "low agriculture" region, will be less affected by anthropogenic modifications overall (at both the local and regional scales) than a lake whose watershed and region both have intensive agriculture. The steps (and results) to test for the presence of this CSI, and its effects on lake nutrients, are described as follows.

Step 1

Our conceptual model of the multi-scaled spatial driver variables of lake total P is informed by the theory and concepts of landscape limnology. Landscape limnology views lakes and other freshwater systems as one piece of the multi-scaled aquatic, terrestrial, and human landscape mosaic (Soranno *et al.* 2010), all of which makes up the macrosystem. Using this framework and findings from past studies, we identified the multi-scaled driver variables that we hypothesized to affect the focal response variable, lake P. Our conceptual model of the local and regional features that were most likely to be related to P (Figure 4a) included: lake depth (Taranu and Gregory-Eaves 2008), the ratio of the watershed-to-lake area (ie drainage ratio; Prepas *et al.* 2001), groundwater potential (Devito *et al.* 2000), local and regional agriculture (Taranu and Gregory-Eaves 2008), local urban cover (Frost *et al.* 2009), and the CSI between regional agriculture and local wetland effects. Given the results from past studies, we did not expect the driver variables

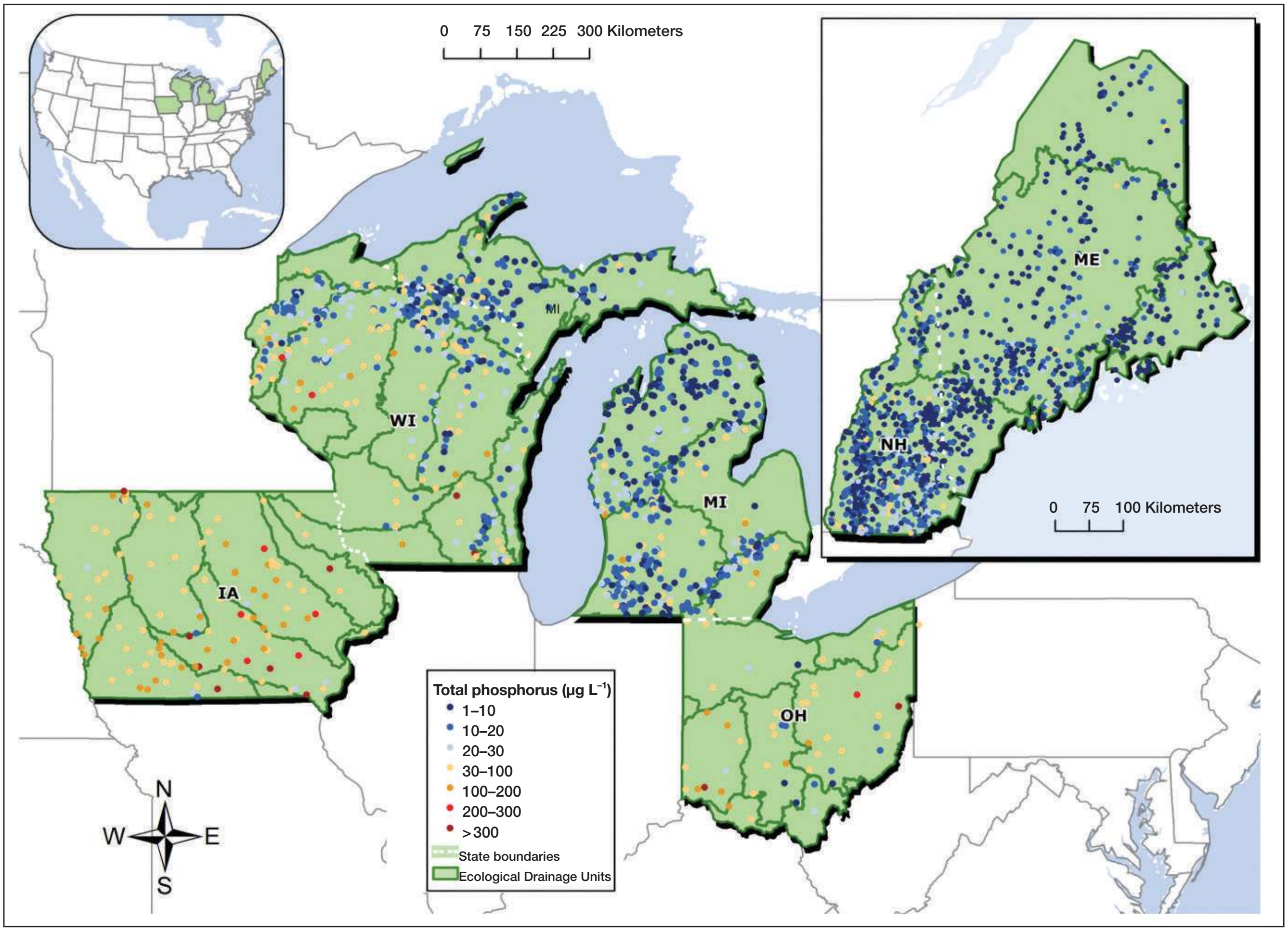

Figure 5. *Map of the lakes used in the case study, the boundaries of the 35 regions defined by Ecological Drainage Units. These regions range in area from 2800 to 49 000 km^2 (mean: 18 500 km^2; standard deviation: 10 300 km^2). Lakes are shown as dots, with the color representing P concentration. The six states in the study area include Iowa, Wisconsin, Michigan, Ohio, New Hampshire, and Maine.*

to exhibit nonlinear relationships with the response variable.

Step 2

We compiled lake nutrient data for 2100 lakes across the Midwest and northeastern US into a single database (Figure 5). Data came from six state management agencies (Iowa, Wisconsin, Michigan, Ohio, New Hampshire, and Maine) that followed federally approved laboratory and field protocols and represent single-point measures of nutrients during summer stratification (individual datasets are described in Webster *et al.* [2008] and Wagner *et al.* [2011]). We also gathered aquatic, terrestrial, and human landscape information from national-scale geographic information systems (GIS) datasets (eg National Hydrography Dataset, National Land Cover Dataset) and integrated them with the lake nutrient database. Landscape data were quantified at two spatial scales: local and regional. Local features were quantified within a 500-m buffer around lakes, a measure that is strongly correlated with landscape features in the watershed (Fergus *et al.* 2011). Regional features were quantified within the Ecological Drainage Unit, a regionalization framework developed to classify freshwater ecosystems based on hydrologic, physiographic, and climatic features (Higgins *et al.* 2005). This database captured sufficient spatial heterogeneity in terms of P within and across the 35 regions so we could address our multi-scaled research questions (Cheruvelil *et al.* 2013).

Step 3

We translated the conceptual model in Figure 4a into a Bayesian hierarchical model. The response variable was $\log_e$-transformed P concentration in 2100 lakes in the 35 different regions (Figure 5). The driver variables were features measured at local, regional, or both scales (Figure 4a), as well as an interaction term between local % wetlands and regional % agriculture (ie the hypothesized CSI). We hypothesized that the slope estimates from the local % wetland–lake P relationship would differ by region and that regional % agriculture would explain some of the variation in these slopes.

We found good evidence in support of the hypothesized CSI (Figure 4c). There was substantial variation in the slopes of the relationship between local % wetlands and P across the regions, with slopes that were either

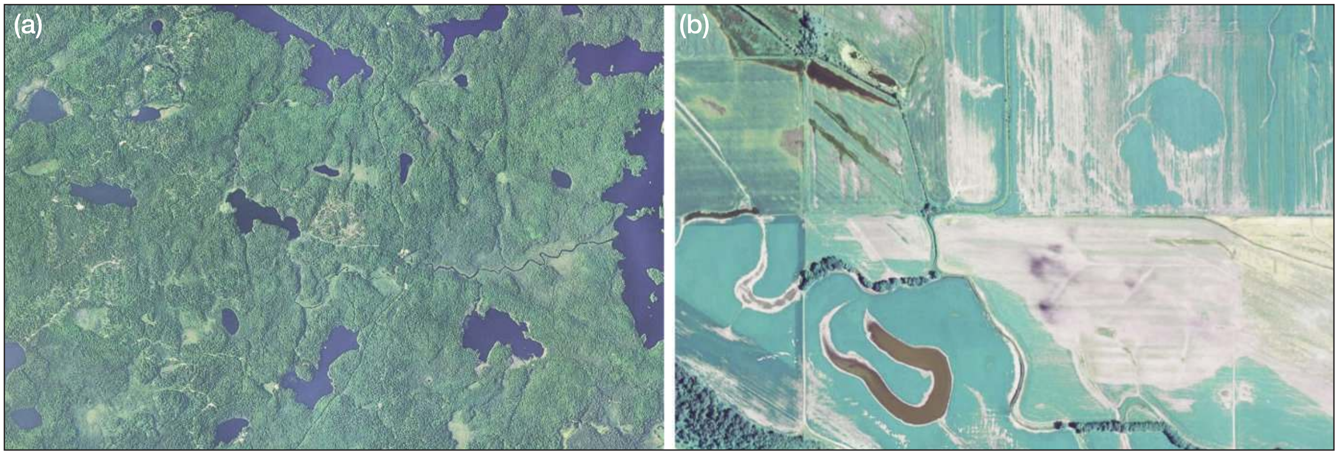

Figure 6. *Images from our study area showing the different landscape settings of (a) low and (b) high regional % agriculture. Images from The National Map – Orthoimagery, US Geological Survey, http://nationalmap.gov/ortho.html.*

positive, negative, or zero (Figure 4b). In regions with low % agriculture, local wetlands were positively associated with P; whereas, in regions with high % agriculture, local wetlands were negatively associated with P (Figure 4c). The differential effects of local % wetlands on P were not due to an interaction between local % agriculture and local % wetlands (CEF unpublished data); rather, it was the interaction *across* scales that mattered (Figure 4c). Regional % agriculture accounted for some of the variation in the wetland–P slope differences across regions, with the 95% credible interval for the CSI parameter in the model not overlapping zero (posterior mean = –1.19, 95% credible interval = –2.34, –0.02; 80% credible interval = –2.17, –0.22). This CSI between local wetlands and regional agriculture was linear, as expected; the data show a linear relationship between regional agriculture and the region-specific wetland–P slope (Figure 4c). If we had ignored the regional variation in this relationship, we would have detected no effect of local wetlands on P because the overall slope of the relationship across the entire dataset was weak, with a 95% credible interval including zero (blue line in Figure 4b).

We can use these results to develop additional hypotheses to help explain variations in P and improve our understanding of these macrosystems. One interpretation of the results is that in regional settings dominated by agriculture, wetlands act as a P "sink" on the landscape, retaining excess P before it enters lakes (Figure 6). However, the spatial arrangement and hydrological connectivity of wetlands in the watershed are likely to be important at the local scale. Therefore, future work should examine the importance of connectivity in wetland–P relationships by developing freshwater connectivity metrics that better capture mechanistic P–water transport relationships at the local scale. For instance, we hypothesize that freshwater connectivity differs in regions with different levels of human disturbance and could be important in better understanding fine-scaled relationships across regions.

■ Applying CSI research to management and policy

As macrosystem ecologists identify and quantify interactions underlying environmental problems, many of which are multi-scaled, they will be able to play an increasingly important role in developing sound policy and management strategies (Carpenter and Turner 2000; Peters *et al.* 2008). By identifying the most important environmental gradients and CSIs driving valued ecosystem response variables (as per steps described in Peters *et al.* [2008]), researchers can, by logical extension, determine in what contexts modeled relationships can be translated from one region or time period to another. Improved understanding of CSIs may facilitate better identification of individual ecosystems and regions that are particularly vulnerable to human impacts, and therefore might need stronger protection or different management approaches than less vulnerable systems or regions. Finally, because knowledge of CSIs defines the spatial and temporal bounds within which particular modeled relationships apply, management agencies can strive to align policy with the spatial/temporal structures defined by CSIs.

Our results demonstrate how a CSI between regional land use and local wetlands affects lake water quality, showing that one-size-fits-all management decisions will often be ineffective. Such an approach inappropriately assumes that cause–effect relationships between system response variables and driver variables are the same across broad geographic extents and through time. Our example shows that local understanding (eg identifying the relationship between local wetlands and lake nutrients) and decisions within a region (eg which wetlands to prioritize for protection) can be informed by incorporating regional-scale attributes (eg regional agricultural land use) into a multi-scaled framework that uses information from a broad geographic area.

Looking to the future, we anticipate many management scenarios that will benefit from considering environmental problems at broader spatial (and temporal) extents than have conventionally been used by researchers and resource managers. Although criteria for managing freshwater nutrients in the US are mainly determined at the state level, results from our six-state analysis highlight the usefulness of considering extents beyond individual state (political) boundaries. For instance, P within Michigan lakes, one of the states included in our study, varies relatively little among regions (Cheruvelil *et al.* 2008); yet across multiple states, there is much more among-region variation in P (Cheruvelil *et al.* 2013). Thus, region-specific management of P may not be warranted at the state level but recognition of broader-scale variation, effectively captured at the regional scale, could aid coordination among states and with federal agencies, with the aim of fostering consistent management approaches, criteria, and evaluation across the country.

Considering and measuring CSIs could also substantially contribute to research and management efforts to assess ecosystem health through the use of biological monitoring. To date, many such efforts have been conducted in a way that is specific to a particular region and ecosystem type, with little capacity to synthesize across studies. More explicit studies, both within and across regions, could improve our understanding of the spatial variation of biotic responses to hydrogeomorphic features, anthropogenic stressors, and CSIs among these drivers. Ultimately, our approach for investigating CSIs can serve as a basis for efforts to understand a wide variety of multi-scaled problems, such as climate change, land-use/land-cover change, and invasive species.

Conclusions

We live in a rapidly changing world, yet our understanding of the ecological consequences of broad-scale changes in land use, biogeochemical cycles, and climate is still incomplete. CSIs related to these changes are one of the key knowledge gaps in macrosystems ecology. We need to identify the conditions or the environments prone to CSIs, so it will be possible to anticipate, manage, and respond to current environmental change. Unfortunately, because ecologists have only just begun to quantify CSIs, there are too few examples to generalize about the ecosystem properties and the important scales that lead to them. To do so, ecologists must promote initiatives to coordinate any type of data-gathering efforts that provide multi-scaled, open-source data at broad spatial extents for relevant drivers and response variables needed to quantify CSIs.

Macrosystems, by definition, are multi-thematic, multi-scaled, and have processes that operate across space and time (Heffernan *et al.* 2014). Such macrosystem characteristics, along with their CSIs, can be difficult to incorporate into conceptual models, database design and development, and analytical approaches. Because individual scientists cannot have all of the technical skills and disciplinary expertise required for such work (Levy *et al.* 2014), it will be commonplace for these types of studies to be conducted by relatively large, interdisciplinary, collaborative teams. Although generally experienced in the use of analytical tools such as modeling and statistics, ecologists only rarely receive training in the ecoinformatics tools needed to work with such large and complex collections of data (Rüegg *et al.* 2014) or in the skills essential to operate in the highly collaborative environments necessary to study macrosystems (Cheruvelil *et al.* 2014); even more rarely do they obtain sufficient credit for participating and contributing to such efforts (Goring *et al.* 2014). More cross-disciplinary education programs and changes in our institutions are needed to train and support the next generation of macrosystems ecologists.

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References

Burnham KP and Anderson DR (Eds). 2002. Model selection and multi-model inference: a practical information-theoretic approach. New York, NY: Springer-Verlag.

Carpenter SR and Turner MG. 2000. Hares and tortoises: interactions of fast and slow variables in ecosystems. *Ecosystems* **3**: 495–97.

Cheruvelil KS, Soranno PA, Bremigan MT, *et al.* 2008. Grouping lakes for water quality assessment and monitoring: the roles of regionalization and spatial scale. *Environ Manage* **41**: 425–40.

Cheruvelil KS, Soranno PA, Weathers KC, *et al.* 2014. Creating and maintaining high-performing collaborative research teams: the importance of diversity and interpersonal skills. *Front Ecol Environ* **12**: 31–38.

Cheruvelil KS, Soranno PA, Webster KE, and Bremigan MT. 2013. Multi-scaled drivers of ecosystem state: quantifying the importance of the regional spatial scale. *Ecol Appl* **23**: 1603–18.

Cole JJ, Carpenter SR, Kitchell JF, *et al.* 2002. Pathways of organic carbon utilization in small lakes: results from a whole-lake ^{13}C addition and coupled model. *Limnol Oceanogr* **47**: 1664–75.

Cressie N, Calder CA, Clark JS, *et al.* 2009. Accounting for uncertainty in ecological analysis: the strengths and limitations of hierarchical statistical modeling. *Ecol Appl* **19**: 553–70.

Devito KJ, Creed IF, Rothwell RL, *et al.* 2000. Landscape controls on phosphorus loading to boreal lakes: implications for the potential impacts of forest harvesting. *Can J Fish Aquat Sci* **57**: 1977–84.

Fergus CE, Soranno PA, Cheruvelil KS, *et al.* 2011. Multi-scale landscape and wetland drivers of lake total phosphorus and water color. *Limnol Oceanogr* **56**: 2127–46.

Frost PC, Kinsman LE, Johnston CA, *et al.* 2009. Watershed discharge modulates relationships between landscape components and nutrient ratios in stream seston. *Ecology* **90**: 1631–40.

Gelman A and Hill J (Eds). 2007. Data analysis using regression and multilevel/hierarchical models. New York, NY: Cambridge University Press.

Goring SJ, Weathers KC, Dodds WK, *et al.* 2014. Improving the culture of interdisciplinary collaboration in ecology by expanding measures of success. *Front Ecol Environ* **12**: 39–47.

Gunderson LH and Holling CS (Eds). 2002. Panarchy: understanding transformations in human and natural systems. Washington, DC: Island Press.

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.

Higgins JV, Bryer MT, Khoury ML, *et al.* 2005. A freshwater classification approach for biodiversity conservation planning. *Conserv Biol* **19**: 432–45.

Levy O, Ball BA, Bond-Lamberty B, *et al.* 2014. Approaches to advance scientific understanding of macrosystems ecology. *Front Ecol Environ* **12**: 15–23.

Ludwig JA, Bartley R, Hawdon AA, *et al.* 2007. Patch configuration non-linearly affects sediment loss across scales in a grazed catchment in North-east Australia. *Ecosystems* **10**: 839–45.

Michener WK and Jones MB. 2012. Ecoinformatics: supporting ecology as a data-intensive science. *Trends Ecol Evol* **27**: 85–93.

Miller JR, Turner MG, Smithwick EAH, *et al.* 2004. Spatial extrapolation: the science of predicting ecological patterns and processes. *BioScience* **54**: 310–20.

Peters DPC, Bestelmeyer BT, and Knapp AK. 2011. Perspectives on global change theory. In: Scheiner SM and Willig MR (Eds). The theory of ecology. Chicago, IL: University of Chicago Press.

Peters DPC, Bestelmeyer BT, and Turner MG. 2007. Cross-scale interactions and changing pattern–process relationships: consequences for system dynamics. *Ecosystems* **10**: 790–96.

Peters DPC, Groffman PM, Nadelhoffer KJ, *et al.* 2008. Living in a connected world: a framework for continental-scale environmental science. *Front Ecol Environ* **5**: 229–37.

Peters DPC, Pielke RA, Bestelmeyer BT, *et al.* 2004. Cross-scale interactions, nonlinearities, and forecasting catastrophic events. *P Natl Acad Sci USA* **101**: 15130–35.

Pielke RA, Adegoke J, Beltran-Prqekurat A, *et al.* 2007. An overview of regional land-use and land-cover impacts on rainfall. *Tellus* **59B**: 587–601.

Prepas EE, Planas D, Gibson JJ, *et al.* 2001. Landscape variables influencing nutrients and phytoplankton communities in Boreal Plain lakes of northern Alberta: a comparison of wetland- and upland-dominated catchments. *Can J Fish Aquat Sci* **58**: 1286–99.

Qian SS, Cuffney TF, Alameddine I, *et al.* 2010. On the application of multilevel modeling in environmental and ecological studies. *Ecology* **91**: 355–61.

Rüegg J, Gries C, Bond-Lamberty B, *et al.* 2014. Completing the data life cycle: using information management in macrosystems ecology research. *Front Ecol Environ* **12**: 24–30.

Soranno PA, Cheruvelil KS, Webster KE, *et al.* 2010. Using landscape limnology to classify freshwater ecosystems for multiecosystem management and conservation. *BioScience* **60**: 440–54.

Stow CA, Jolliff J, McGillicuddy D, *et al.* 2009. Skill assessment for coupled biological/physical models of marine systems. *J Marine Syst* **76**: 4–15.

Taranu ZE and Gregory-Eaves I. 2008. Quantifying relationships among phosphorus, agriculture, and lake depth at an interregional scale. *Ecosystems* **11**: 715–25.

Tranvik LJ, Downing JA, Conter JB, *et al.* 2009. Lakes and reservoirs as regulators of carbon cycling and climate. *Limnol Oceanogr* **54**: 2298–314.

Vergara PM and Armesto JJ. 2009. Responses of Chilean forest birds to anthropogenic habitat fragmentation across spatial scales. *Landscape Ecol* **24**: 25–38.

Wagner T, Soranno PA, Webster KE, *et al.* 2011. Landscape drivers of regional variation in the relationship between total phosphorus and chlorophyll. *Freshwater Biol* **56**: 1811–24.

Webster KE, Soranno PA, Cheruvelil KS, *et al.* 2008. An empirical evaluation of the nutrient color paradigm for lakes. *Limnol Oceanogr* **53**: 1137–48.

Weller CM, Watzin MC, and Wang D. 1996. Role of wetlands in reducing phosphorus loading to surface water in eight watersheds in the Lake Champlain Basin. *Environ Manage* **20**: 731–39.

Williamson CE, Saros JE, and Schindler DW. 2009. Sentinels of change. *Science* **323**: 887–88.

Willig MR, Bloch CP, Brokaw N, *et al.* 2007. Cross-scale responses of biodiversity to hurricane and anthropogenic disturbance in a tropical forest. *Ecosystems* **10**: 824–38.

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