esa ECOSPHERE

The statistical power to detect cross-scale interactions at macroscales

Tyler Wagner,[1,†] C. Emi Fergus,[2] Craig A. Stow,[3] Kendra S. Cheruvelil,[2,4] and Patricia A. Soranno[2]

[1]U.S. Geological Survey, Pennsylvania Cooperative Fish and Wildlife Research Unit, The Pennsylvania State University, University Park, Pennsylvania 16802 USA
[2]Department of Fisheries and Wildlife, Michigan State University, East Lansing, Michigan 48824 USA
[3]NOAA Great Lakes Laboratory, Ann Arbor, Michigan 48108 USA
[4]Lyman Briggs College, Michigan State University, East Lansing, Michigan 48825 USA

Citation: Wagner, T., C. E. Fergus, C. A. Stow, K. S. Cheruvelil, and P. A. Soranno. 2016. The statistical power to detect cross-scale interactions at macroscales. Ecosphere 7(7):e01417. 10.1002/ecs2.1417

Abstract. Macroscale studies of ecological phenomena are increasingly common because stressors such as climate and land-use change operate at large spatial and temporal scales. Cross-scale interactions (CSIs), where ecological processes operating at one spatial or temporal scale interact with processes operating at another scale, have been documented in a variety of ecosystems and contribute to complex system dynamics. However, studies investigating CSIs are often dependent on compiling multiple data sets from different sources to create multithematic, multiscaled data sets, which results in structurally complex, and sometimes incomplete data sets. The statistical power to detect CSIs needs to be evaluated because of their importance and the challenge of quantifying CSIs using data sets with complex structures and missing observations. We studied this problem using a spatially hierarchical model that measures CSIs between regional agriculture and its effects on the relationship between lake nutrients and lake productivity. We used an existing large multithematic, multiscaled database, LAke multiscaled GeOSpatial, and temporal database (LAGOS), to parameterize the power analysis simulations. We found that the power to detect CSIs was more strongly related to the number of regions in the study rather than the number of lakes nested within each region. CSI power analyses will not only help ecologists design large-scale studies aimed at detecting CSIs, but will also focus attention on CSI effect sizes and the degree to which they are ecologically relevant and detectable with large data sets.

Key words: chlorophyll *a*; cross-scale interactions; lake; land use/cover; statistical power; total nutrients.

Received 20 April 2016; accepted 26 April 2016. Corresponding Editor: D. P. C. Peters.

† **E-mail:** txw19@psu.edu

Introduction

Ecological systems are shaped by processes operating at multiple temporal and spatial scales, and this hierarchical structure can make it challenging to understand ecological dynamics (Levin 1992). Cross-scale interactions (CSIs), whereby ecological processes operating at one spatial or temporal scale interact with processes operating at another scale, can promote ecological complexity and lead to unexpected patterns if multiscaled relationships are ignored (Peters et al. 2004, 2007, Heffernan et al. 2014, Soranno et al. 2014). These complex, multiscaled relationships can make it difficult to manage systems and predict how they may respond to broadscale drivers of change such as climate change and land-use conversion.

As multiscale perspectives develop, attention toward CSIs, and their potential influence on ecological complexity, will likely continue to grow among various disciplines in ecology (Cash et al. 2006, Vergara and Armesto 2009, Koo et al. 2014, Menge et al. 2015). For example, CSIs are hypothesized to be critical to understand complex forest ecological dynamics in the face of multiscaled disturbance regimes, climate change, and management actions (Becknell et al. 2015). In aquatic systems, broadscale ecosystem characteristics and fine-scale microhabitat characteristics likely interact to influence littoral benthic communities (Stoffels et al. 2005). Further, CSIs are important not only to biological and biogeochemistry responses in systems but also to disturbance phenomena such as fire regime, which are influenced by multiscaled spatial and temporal factors and processes (Falk et al. 2007).

Empirical evidence for the presence of CSIs is also growing across different ecological systems. For example, in terrestrial systems red spruce growth is influenced by an interaction between local-scale topography and regional-scale climatic factors (Koo et al. 2014). In aquatic systems, CSIs are shown to influence ecological responses such as brook trout *Salvelinus fontinalis* occupancy (DeWeber and Wagner 2015), marine intertidal community composition (Menge et al. 2015), and lake water chemistry (Fergus et al. 2011). There is also evidence that the well-studied empirical relationships between lake phosphorus and chlorophyll *a* (CHL; a measure of lake primary production) concentrations are influenced by CSIs with regional agriculture and wetland presence (Wagner et al. 2011, Filstrup et al. 2014), which may help reconcile differences in relationships among different studies.

Although CSIs may be conceptually and ecologically important to understand ecological complexities, there are data demands and analytical challenges for quantifying these relationships (Soranno et al. 2014). To quantify CSIs, there is a need for multithematic data sets that span potentially extensive spatial and/or temporal scales, depending on the ecological phenomena of interest (Koo et al. 2014, Soranno et al. 2014, Keane et al. 2015). Because these sorts of data sets are rare, frequently multiple data sets from different sources are compiled to create a multithematic, multiscaled data set to examine CSIs (Soranno et al. 2015). The consequences of this approach are "messy" data sets with complex (e.g., uneven numbers of observations across spatial or temporal extents) and multilevel data structures.

Hierarchical models represent one analytical approach that can accommodate the multilevel data structures observed in multithematic, multiscaled data sets and that can be used to estimate CSIs. In fact, hierarchical models have been used to quantify CSIs in both the ecological and social sciences (Mathieu et al. 2012, Soranno et al. 2014, Dixon Hamil et al. 2016). Although factors affecting the statistical power of hierarchical models generally (Scherbaum and Ferreter 2009) and specifically related to detecting CSIs (Snijders and Bosker 1993, Mathieu et al. 2012) have been studied, these investigations have not been in ecological disciplines. To the best of our knowledge, the effect of such multilevel data structures on the statistical power to detect CSIs has yet to be evaluated within the context of macroscale investigations of ecological CSIs.

In this study, we examine the ability to detect CSIs under different scenarios that may be encountered with multiscaled, compiled data sets (e.g., spatially varying sample sizes, varying CSI effect sizes, and different variance parameters). We studied this problem using a spatially hierarchical model that measures CSIs between driver variables (as described in Soranno et al. 2014). These types of CSIs have an interaction between a higher-level variable (e.g., regional agriculture) on a lower-level driver variable (e.g., lake nutrients) on the response (e.g., lake chlorophyll concentrations). We focused on evaluating CSIs between regional agricultural land use and the effects of lake nutrients (i.e., phosphorus and nitrogen) on lake chlorophyll concentrations (a measure of primary producer biomass) because previous work has demonstrated the potential for regional land use to mediate the effects of lake nutrients on primary producer biomass, resulting in a CSI (Wagner et al. 2011, Filstrup et al. 2014). Specifically, previous studies have demonstrated a CSI between regional agricultural land use and the rate at which chlorophyll concentrations increase with increasing nutrients, such as phosphorus concentrations (Wagner et al. 2011). The mechanisms for this CSI are hypothesized to be due to simultaneous nitrogen and phosphorus enrichment and to the export of more biologically available forms of nutrients in agriculturally dominated regions compared to regions with other land cover types (Filstrup et al. 2014). We used a spatially extensive lake water chemistry database, LAke multiscaled GeOSpatial and temporal database (LAGOS; Soranno et al. 2015), to parameterize the power analysis simulations. This type of power analysis can help inform study designs to formally examine such complex, multiscaled relationships in ecology. We also suggest that a power analysis for CSIs is important for understanding what CSI effect sizes are ecologically relevant and detectable.

Methods

Lake and land-use data

Data used to derive estimates for parameterizing power analysis simulations came from the LAGOS database, a multithematic lake database that integrates lake water chemistry data ($\text{LAGOS}_{\text{LIMNO}}$) and geospatial data ($\text{LAGOS}_{\text{GEO}}$) across the Midwest and Northeast regions of the United States (Soranno et al. 2015). We used $\text{LAGOS}_{\text{LIMNO}}$ version 1.0541 and $\text{LAGOS}_{\text{GEO}}$ version 1.03 for our analyses.

We used a subset of lakes (≥4 ha and <10,000 ha in surface area) from LAGOS that had measurements for CHL, total phosphorus (TP; n = 3781 lakes), and total nitrogen (TN; n = 3107 lakes). To reduce intraseasonal variation in nutrients within lakes, we used summer epilimnetic (15 June–15 September) average nutrient concentrations for data collected between 2002 and 2011 (the 10 most recent years of data available), which resulted in one observation per lake. The number of years that were sampled for each lake ranged from 1 to 10 yr for both TP and TN, with a median number of years of two for TP and one for TN. The standard deviation in annual TP for lakes that were sampled more than one year ranged from 0 to 518 μg/L, with a median of 3.5 μg/L. The standard deviation in annual TN for lakes that were sampled more than one year ranged from 0 to 5155 μg/L, with a median of 116 μg/L. The U.S. Geological Survey four-digit Hydrologic Unit (HU), which is based on river basins (Seaber et al. 1987), was used as a regionalization framework to group lakes on the landscape. The proportion of agricultural land use in each region was calculated from the 2006 National Land Cover Dataset (Fry et al. 2011).

Statistical model: CSIs between regional agriculture and the effect of nutrients on lake productivity

Quantifying CSIs requires multiscale analytical frameworks such as spatially explicit landscape models, systems models, and statistical models (Koo et al. 2014, Nash et al. 2014, Dixon Hamil et al. 2016, Keane et al. 2015). Hierarchical models are one statistical approach to quantify CSIs among driver variables, as defined in Soranno et al. (2014). Hierarchical models are well suited to study CSIs among driver variables because they partition variation in ecological responses among hierarchically structured spatial units that can be related to multiscaled drivers and CSIs among these drivers (Soranno et al. 2014, Dixon Hamil et al. 2016).

We defined CSIs similar to previous studies (Filstrup et al. 2014, Soranno et al. 2014, DeWeber and Wagner 2015) using a varying intercept, varying slope hierarchical model that included predictor variables at two levels (Level 1: observation level [lake level] and Level 2: group level [region level] of the hierarchical model). The basic data structure for this CSI model specification is multiple observations of response and predictor variables of interest for individual systems (e.g., lakes) grouped spatially in an ecologically relevant manner using a regionalization framework (Cheruvelil et al. 2013). Each lake had at least one observation for each of the three lake chemistry variables, TP, CHL, and TN, and was grouped spatially into regions. The varying intercepts in the hierarchical model allowed the group of lakes in each region to have their own mean CHL that might differ from the mean CHL for groups of lakes in other regions, while the varying slopes allowed the each region's lakes to differ in the relationship between TP (or TN) and CHL from that of other regions. A CSI exists if the region-specific slopes in the TP (or TN)–CHL relationship varies predictably with a region-specific predictor variable(s), indicating an interaction between a lake-level (Level 1) and region-level (Level 2) predictor variable whereby the effects of local predictor variables are mediated by this larger scale phenomenon, a CSI. Although more complex model specifications are possible, we focused on a relatively simple, yet ecologically relevant, model:

$$\text{Level 1: } y_i \sim N\left(\alpha_{j(i)} + \beta_{j(i)} \cdot x_i, \sigma_y^2\right), \quad \text{for } i = 1, \ldots n$$

$$\text{Level 2: } \begin{pmatrix} \alpha_j \\ \beta_j \end{pmatrix} \sim \text{MVN}\left(\begin{pmatrix} \gamma_\alpha \\ \gamma_\beta + \gamma_{\beta 1} \cdot z_j \end{pmatrix}, \begin{pmatrix} \sigma_\alpha^2 & \sigma_{\alpha\beta} \\ \sigma_{\alpha\beta} & \sigma_\beta^2 \end{pmatrix}\right), \quad \text{for } j = 1, \ldots J$$

where y_i is the response variable (e.g., $\log_e$ CHL for lake i), x_i is the standardized (mean = 0, SD = 1) lake-level predictor (e.g., $\log_e$ TP [or $\log_e$ TN] for lake i), α_j and β_j are group-specific (e.g., region-specific) intercepts and slopes, and σ_y^2 is the model error term variance. The region-specific intercepts and slopes are assumed to come from a multivariate normal distribution (MVN), where γ_α is the grand mean intercept and γ_β and $\gamma_{\beta 1}$ are the intercept and slope describing the relationship between the region-level predictor variable, z_j, and the slopes in the relationship between x and y. The parameters σ_α^2, σ_β^2, and $\sigma_{\alpha\beta}$ are the variances among intercepts and slopes, and the covariance, respectively. The parameter $\gamma_{\beta 1}$ describes the CSI. We fitted TP–CHL and TN–CHL models with the percentage of agriculture land use in each region as the region-level predictor (z_j). These models provided parameter estimates used in the data-generating process for the power analysis simulations (see *Power analysis simulations* below). All analyses were performed using the lmer function in the program R (Bates et al. 2014: R library lme4, R Core Team 2015).

Power analysis simulations

We used a simulation approach to assess the statistical power to detect CSIs. This process consisted of two steps: a data-generating step and an estimation step. For the data-generating step, the varying intercept, varying slope model (Eq. 1) was used as the data-generating model. All parameters in this model, as well as the number of observations, n, and number of regions, J, used to generate simulated data sets could be manipulated to assess their relative influence on the power to detect CSIs. For example, one important question related to detecting CSIs is: "How large of an effect size for the CSI can we detect given the variability observed across the landscape and given the number of ecosystems and regions with data?" Within the simulation context, this question is addressed by holding all parameters at their estimated values (i.e., the values estimated from the LAGOS database) and increasing or decreasing the value we assume for the CSI (e.g., change the value of $\gamma_{\beta 1}$ used in the data-generating step) to examine the effects on power.

The estimation step of the power analysis consisted of fitting the varying intercept, varying slope model to 1000 simulated data sets and determining whether the CSI was detected (i.e., if $\hat{\gamma}_{\beta 1}$ was statistically discernible from zero). Because the data were generated assuming a slope for the CSI that differed from zero, the null hypothesis of a zero slope is false, and power was estimated as the percentage of simulations (of 1000) that rejected the null hypothesis (Wagner et al. 2007, see Appendix S1: Data S1 for R code). Because we simulated positive CSIs in all power analyses, the estimated CSI was considered significant if the lower bound of the 95% confidence interval (CI) for $\gamma_{\beta 1}$ exceeded zero. For the rare cases ($\leq$7% of the 1000 simulations) when some simulated data sets resulted in small sample sizes with fitted models that failed to converge (i.e., parameter estimates were not deemed reliable), those simulations were not used to calculate power.

Power analysis scenarios

For both the TP–CHL and TN–CHL analyses, we investigated the extent to which the following factors affected the ability to detect a CSI: (1) increasing CSI effect size, $\gamma_{\beta 1}$, (2) increasing the number of regions, J, sampled across the landscape, (3) increasing the mean number of lakes, $\bar{n}$, sampled within each region, (4) increasing and decreasing the conditional standard deviation, σ_β, in the CSI regression, and (5) increasing and decreasing the standard deviation σ_y. For (1), we examined the range of region-specific responses of CHL to increases in TP and TN (β_js from the estimates using LAGOS) to determine a range of CSI effect sizes to include in the power analyses. This approach provided a range of percentage increases in CHL that corresponded to a 1% increase in TP or TN, which helped place some ecological bounds on what kind of CHL response might be anticipated when a CSI was present.

Because of the way we defined a CSI, a regionalization framework must be used as the second-level grouping factor in the hierarchical model (i.e., Level 2 of Eq. 1). The choice of regionalization framework, and the resulting number of regions in the data set, is particularly important when estimating CSIs; as the number of regions increases or decreases, the sample size, J, in the second level of the hierarchical model also correspondingly increases or decreases, which is the level where the CSI is being estimated.

This fact is important because power necessarily increases with increasing sample size (Steidl et al. 1997). Therefore, we evaluated (2) by considering scenarios where the number of regions was 10, 15, 20, 35, 40, 50, or 100 in order to span a reasonable range that might be encountered in macrosystems ecology research interested in estimating CSIs.

The number of lakes within a region is also an important consideration when thinking about detecting CSIs, that is, how many systems need data within a region to achieve adequate power? In most cases, all systems in a population of interest cannot be sampled due to logistical and resource constraints (i.e., we cannot perform a complete census). In addition, because many macrosystem investigations into large-scale phenomena like CSIs are contingent on compiled data from many sources (e.g., compiling data from many state agencies and universities; Soranno et al. 2015), we examined the effect of changing the mean number of lakes per region (3) by generating within-region sample sizes as a negative binomial random number, with the mean of the negative binomial ($\bar{n}$) set to the value of interest and the scale parameter set to the value estimated from the observed data. Simulating within-region sample sizes in this manner resulted in most regions with sample sizes near the mean and a few regions with larger sample sizes, which mimicked the structure of the LAGOS data. For example, for lakes with TP–CHL data the distribution of within-region sample sizes was right-skewed (min = 1, 25th percentile = 14, median = 36, mean = 62, 75th percentile = 89, max = 297).

Lastly, we examined how changing the (4) conditional standard deviation, σ_β, in the CSI regression and the (5) residual standard deviation, σ_y, influenced power. The conditional standard deviation, σ_β, represents the residual variation in the Level 2 CSI (i.e., the unexplained "noise" around the CSI regression), whereas the residual standard deviation, σ_y, represents the residual variation in the Level 1 TP or TN–CHL relationship (i.e., the unexplained "noise" around the TP or TN–CHL regression). Because we did not have any values of interest a priori, we evaluated the effect of changing these standard deviations by setting them to their estimated values and to the lower and upper 95% confidence interval values. Parameters not being changed in any given simulation were held at estimated values.

Results

CSIs between regional agriculture and the effect of nutrients on lake productivity

LAGOS summary statistics.—For the TP–CHL analysis, there were 3781 lakes located within 61 regions (HU-4s; Seaber et al. 1987). The number of lakes per region ranged from 1 to 297, with a mean of 62 lakes per region (Fig. 1). Mean TP was 38.7 μg/L and ranged from 1 to 1122 μg/L, whereas mean CHL was 15.8 μg/L and ranged from 0.03 to 549 μg/L. The mean percentage agricultural land use across the 61 regions was 37.4% and ranged from 1.7% to 78.6%. For the TN–CHL analysis, there were 3107 lakes located in 62 regions (Fig. 1). The number of lakes per region ranged from 1 to 284, with a mean of 49 lakes per region. TN ranged from 55 to 11,860 μg/L, with a mean of 849.2 μg/L. Mean CHL was 16.3 μg/L and ranged from 0.15 to 307 μg/L. The mean percentage agricultural land use across the 62 regions was 36.8% and ranged from 1.7% to 78.6%.

Statistical models.—LAGOS data revealed a positive relationship between TP (and TN) and CHL; those relationships were spatially variable, although the relationship between TP and CHL was less variable both within and across regions than the TN–CHL relationship (Fig. 2, Table 1). There was a significant CSI for the TP–CHL relationship ($\hat{\gamma}_{\beta 1}$ = 0.003 [95% CI = 0.001, 0.005]), with increasing regional agriculture land use resulting in an increasing rate of response of CHL to increasing TP (Fig. 2B). For example, at 0% agricultural land use in a region, a 1% increase in TP resulted in a 0.85% increase in CHL. However, in a region with 75% agricultural land use, a 1% increase in TP results in a 1.1% increase in CHL (Fig. 3). Although the CSI effect size is relatively small, it could promote shifts in phytoplankton community composition if increases in agricultural land use result in lower water clarity so that additional chlorophyll is required to capture the available light energy. This relatively small CSI effect size may also have more biological significance once its effects (e.g., on carbon fixation) are scaled up to subcontinental or continental scales. The CSI for the TN–CHL

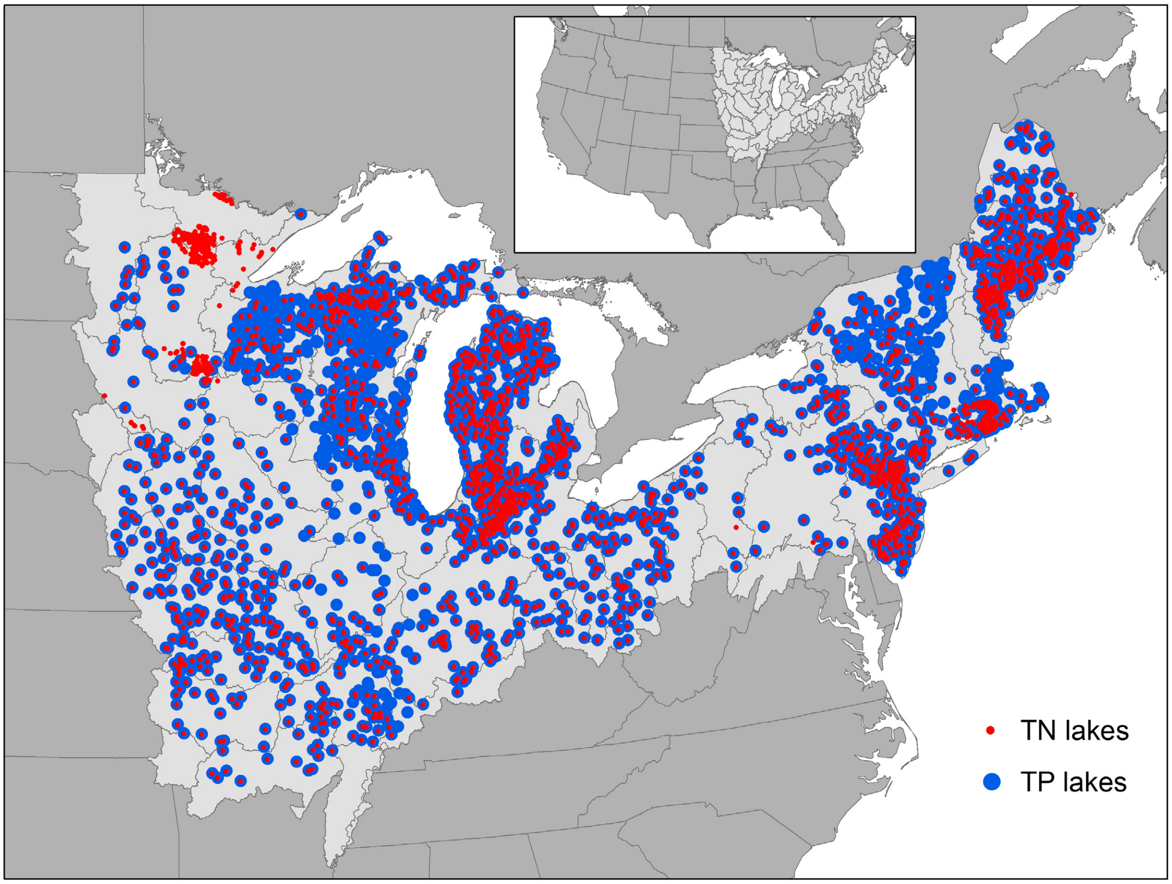

Fig. 1. Map of study lakes. Blue circles indicate lakes with total phosphorus and chlorophyll *a* (CHL) data (n = 3781), and red circles indicate lakes with total nitrogen and CHL data (n = 3107).

relationship was small and not different than zero, with the 95% CI overlapping zero ($\hat{\gamma}_{\beta 1} = 0.0008$ [−0.003, 0.004]; Fig. 2D, Table 1).

Power analysis

The patterns of the relationships between statistical power and changes in effect size, sample size, and model error term variance align with expectations (Mathieu et al. 2012). However, the power analyses provided important insight into the actual magnitude of the CSI effect sizes that could be detected under different sampling scenarios and the influence of Levels 1 and 2 sample sizes and variance terms on detecting macroscale CSIs in freshwater inland lake ecosystems (Table 2). For the TP–CHL analysis, power increased with increasing effect size and number of regions (Fig. 4A). Statistical power was low (less than the conventional 0.8 deemed as adequate power and used as a reference in these analyses; Peterman 1990) when the CSI effect size was low ($\gamma_{\beta 1} = 0.001$), regardless of how many regions were used in the analysis. For the CSI effect size that we estimated from LAGOS ($\gamma_{\beta 1} = 0.003$), power did not reach 0.8 until the number of regions was approximately >50. For large effect sizes ($\gamma_{\beta 1} \geq 0.005$), power was high regardless of the number of regions used in the analysis. A similar pattern in power was observed for the TN–CHL analysis (Fig. 4C); however, power was lower across all effect sizes and number of regions due in part to larger residual variances (as illustrated in Fig. 2C). Although increasing the mean number of lakes sampled within each region increased power, this effect was small compared with increasing the number of regions or increasing the effect size, for both TP–CHL and TN–CHL analyses (Fig. 4B, D).

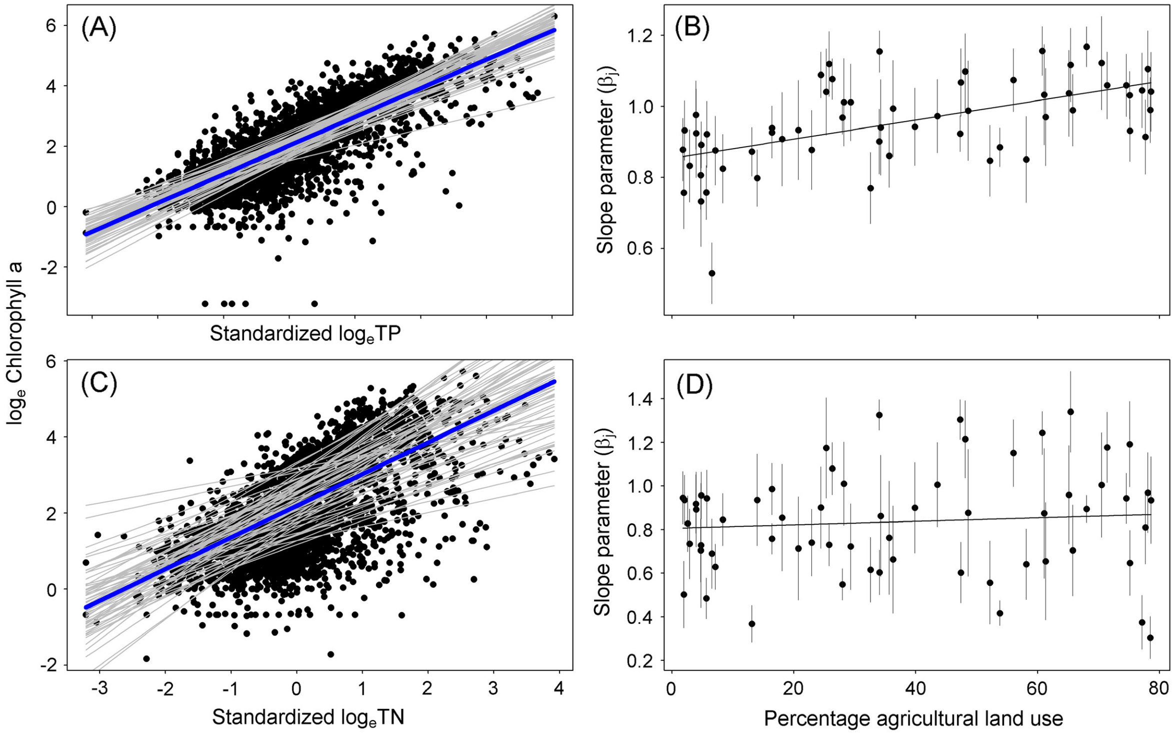

Fig. 2. Relationship between total phosphorus (TP) and chlorophyll *a* (CHL; A) and total nitrogen (TN) and CHL (C). Solid circles in A and C are data points, the thick blue line is the overall relationship between TP or TN and CHL across all lakes, and thin gray lines are region-specific relationships. Panels B and D illustrate the cross-scale interaction between the percentage of agricultural land use in a region and the relationship between TP or TN and CHL (i.e., the relationship between regional percent agriculture and the slopes [$\hat{\beta}_j$] of the TP or TN–CHL relationships). Points are estimated means, vertical bars are ±1 SE, and solid line is hierarchical regression model fit.

Changing the conditional standard deviation, σ_β, influenced power in a predictable manner, with increasing among-region variability in the relationship between TP–CHL and TN–CHL resulting in decreased power (Fig. 5A, C), although the increase in power was negligible for the TN–CHL analyses when the CSI effect size was small (Fig. 5C). Changing the model error term standard deviation, σ_y (i.e., the Level 1 residual standard deviation), had minimal influence on power for both analyses (Fig. 5B, D); however, this pattern partly reflected the parameter values that were used in the analyses (i.e., we chose the estimated value and upper and lower 95% CI as values to investigate, and the residual standard deviation estimate from

Table 1. Estimated parameters used to parameterize power analysis simulations from a varying intercept, varying slope hierarchical model, followed by 95% confidence intervals in parentheses.

	Parameters					
Model	$\hat{\gamma}_\alpha$	$\hat{\gamma}_\beta$	$\hat{\gamma}_{\beta 1}$	$\hat{\sigma}$	$\hat{\sigma}_\alpha$	$\hat{\sigma}_\beta$
TP–CHL	2.00 (1.92, 2.09)	0.85 (0.77, 0.94)	0.003 (0.001, 0.005)	0.68 (0.66, 0.69)	0.27 (0.21, 0.34)	0.14 (0.09, 0.19)
TN–CHL	2.19 (2.03, 2.34)	0.80 (0.64, 0.96)	0.0008 (−0.003, 0.004)	0.76 (0.74, 0.78)	0.59 (0.48, 0.72)	0.30 (0.23, 0.37)

Notes: Separate models were fitted for log$_e$ total phosphorus (TP)–log$_e$ chlorophyll *a* (CHL) and log$_e$ total nitrogen (TN)–log$_e$ CHL relationships. Note that $\hat{\gamma}_{\beta 1}$ is the estimated cross-scale interaction.

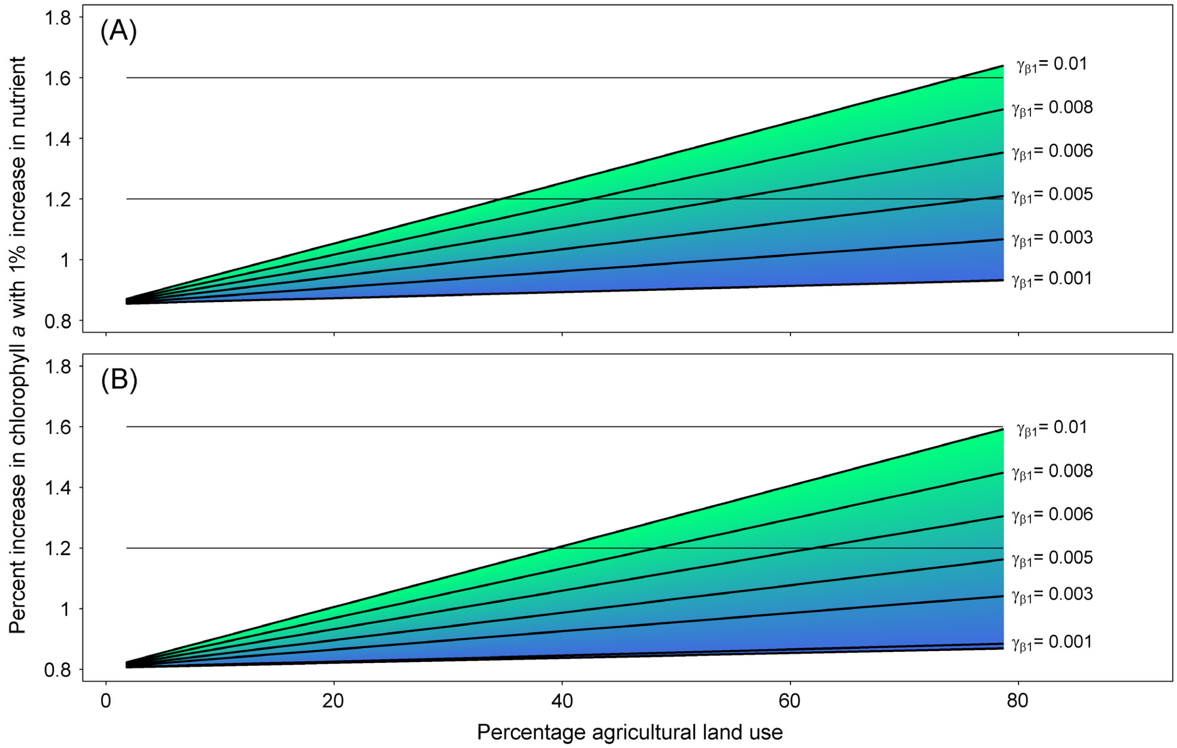

Fig. 3. Effect of increasing the percentage agricultural land use in a region on the rate of increase in chlorophyll *a* (CHL) in response to a 1% increase in total phosphorus (TP; A) or total nitrogen (TN; B) across a range of cross-scale interaction (CSI) effect sizes ($\gamma_{\beta1}$). Effect sizes labeled in figures and corresponding solid lines represent CSI effect sizes examined in power analyses. $\gamma_{\beta1}$ = 0.003 represents the CSI estimated from the data for the TP–CHL relationship. The lowermost solid line in panel B corresponds to the estimated CSI in the TN–CHL relationship ($\gamma_{\beta1}$ = 0.0008), which is shown for comparative purposes, but was not used in the power analyses. A horizontal line at a 1.2% and 1.6% increase in CHL in response to a 1% increase in TP or TN was added to aid in comparing panels.

LAGOS had a relatively narrow CI). However, additional analyses (not reported herein) showed low sensitivity of the power to detect CSIs in response to larger changes in the residual standard deviation, σ_y, as compared to the other factors investigated.

Discussion

Our analysis highlighted several important points. First, estimating CSIs using a hierarchical model requires consideration of sample size at both the level of the individual "system" (e.g., number of lakes within regions) and the level of the region (number of regions). Second, detecting CSIs was much more sensitive to the number of regions used in the analysis as compared to the average number of lakes within regions. This is because the number of regions used in the analysis is the sample size for the second level of the hierarchical model where the CSI is estimated. Thus, expending resources to sample many systems in all regions may not be necessary and resources could be better spent sampling fewer systems across more regions. The relative insensitivity to within-region sample size is likely influenced by the fact that hierarchical models are able to accommodate the spatial imbalance in the number of lakes within each region through the effects of partial pooling (Gelman and Hill 2007). Partial pooling allows estimates of regions to borrow strength from the entire ensemble of data by shrinking the region-specific estimates that are supported by relatively sparse data toward the common mean. In our case study, there were always some regions with

Table 2. Parameter values used in simulation scenarios for estimating the statistical power to detect cross-scale interactions (CSIs).

Scenario	Parameter value
1. CSI effect size ($\gamma_{\beta 1}$)	$\gamma_{\beta 1}$ = 0.001, 0.003, 0.004, 0.006, 0.008, 0.01
2. Level 1 mean sample size ($\bar{n}$)	$\bar{n}$ = 10, 20, 40, 60, 80, 100
3. Level 2 standard deviation (σ_β)	σ_β = 0.228, 0.298, 0.374
4. Level 1 standard deviation (σ_y)	σ_y = 0.738, 0.756, 0.778

Notes: See Eq. 1 for descriptions of model parameters. Parameter values not changed during a simulation were held at estimated values (see Table 1). All scenarios were performed across a range of number of regions, *J*, where *J* = 10, 15, 20, 35, 40, 50, 100. Scenarios 2–4 were performed with a CSI effect size ($\gamma_{\beta 1}$) of 0.001 and 0.003.

many lakes (even if the mean number of lakes per region was small) that helped inform the estimates for data-poor regions.

We also documented the importance of considering within-region and between-region variabilities with respect to detecting CSIs. The power to detect CSIs was sensitive to changes in the variability in the nutrient–CHL and the CSI (slope–regional agriculture) relationships (i.e., the Levels 1 and 2 standard deviations). As with the sample size results, statistical power was more sensitive to changes in regional (Level 2) variability as compared to within-region (Level 1) variability. Thus, if detecting CSIs is the objective of a study, then the allocation of resources in terms of how the landscape is sampled is an important consideration. This type of trade-off is similar to that observed for other ecological questions, such as detecting regional temporal trends in a variable of interest. The trade-off in this case is whether to devote more resources to obtain a precise estimate of each system's status in each year or to obtain less precise estimates of status and sample more systems in each year. If regional trend detection is the goal, resources are better spent on sampling more systems versus

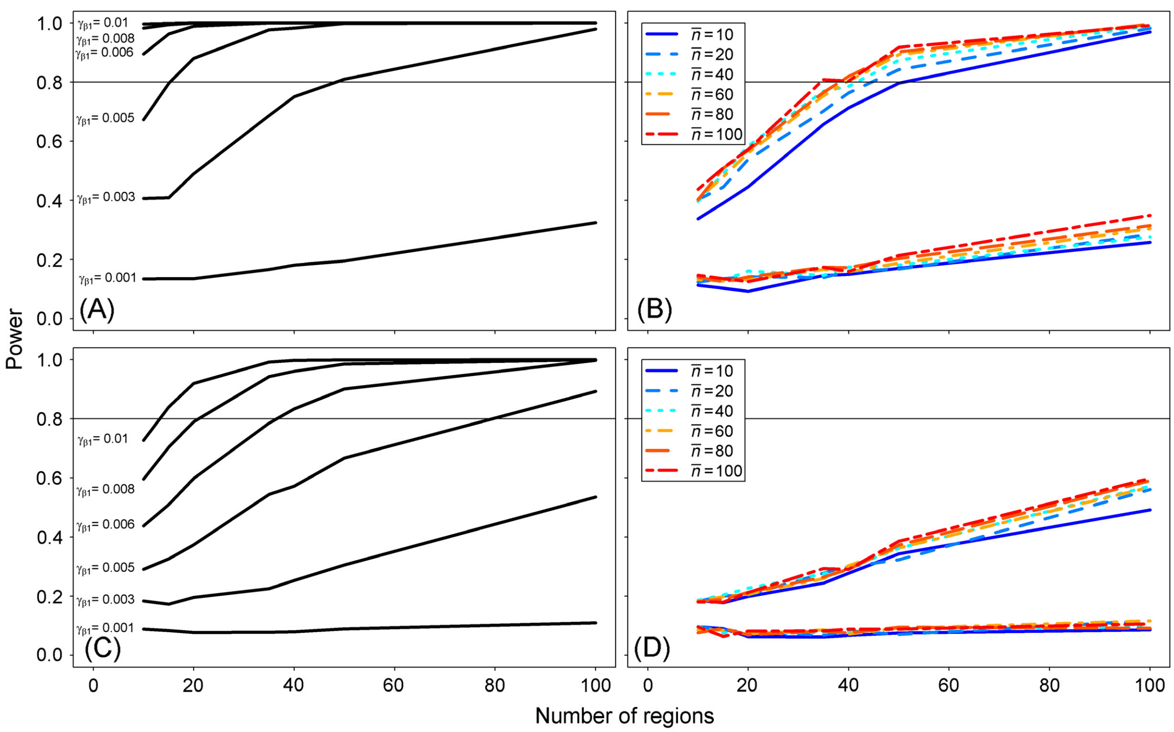

Fig. 4. Power curves for detecting cross-scale interactions (CSIs) with increasing trend magnitude ($\gamma_{\beta 1}$) and mean number of lakes ($\bar{n}$) sampled within each region for the total phosphorus (TP)–chlorophyll *a* (CHL; A, B) and total nitrogen (TN)–CHL relationships (C, D) across a range of region numbers. The CSI is the effect of increasing the proportion of regional agricultural land use on the slope of the TP–CHL and TN–CHL relationships. In panels B and D, the upper set of curves are for $\gamma_{\beta 1}$ = 0.003 and the lower set of curves are for $\gamma_{\beta 1}$ = 0.001.

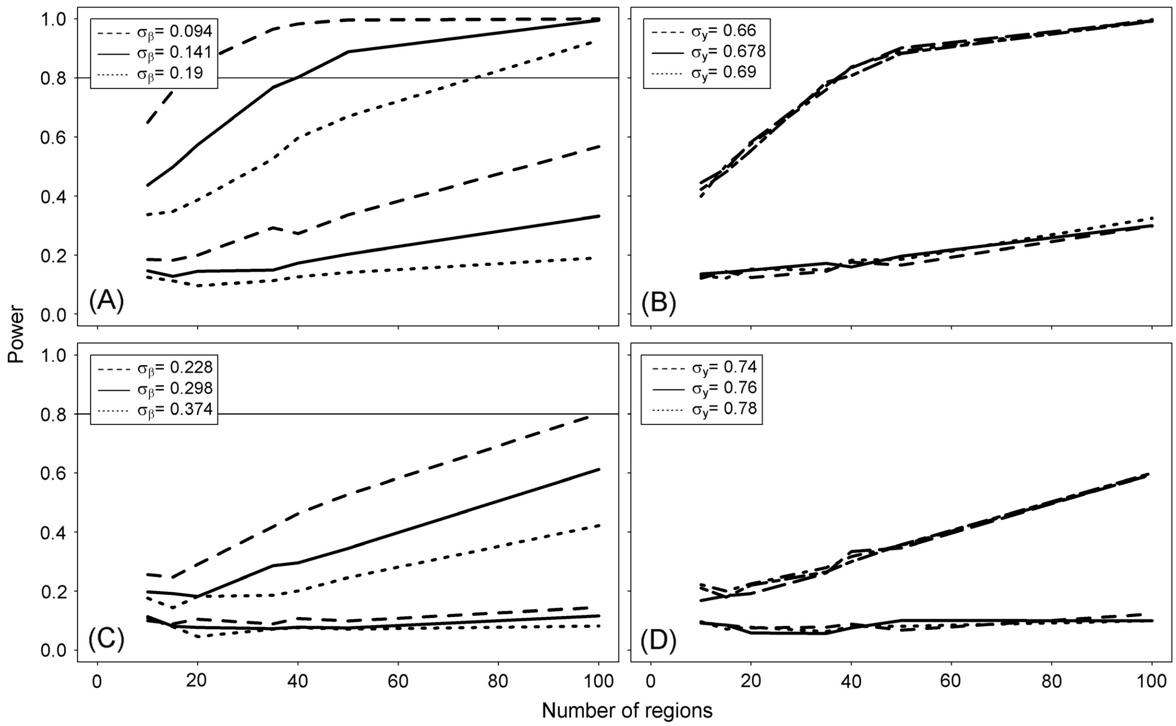

Fig. 5. Power curves for detecting cross-scale interactions (CSIs) with increasing conditional standard deviation (σ_β) in the CSI regression in the total phosphorus (TP)–chlorophyll *a* (CHL; A) and total nitrogen (TN)–CHL (C) models and residual variation (σ_y) (B: TP–CHL; D: TN–CHL) across a range of region numbers. The CSI is the effect of increasing the proportion of regional agricultural land use on the slope of the TP–CHL and TN–CHL relationships. The upper set of curves are for $\gamma_{\beta 1}$ = 0.003 and the lower set of curves are for $\gamma_{\beta 1}$ = 0.001.

obtaining a more precise estimate of each system (Wagner et al. 2007).

Estimating CSIs at macroscales is becoming increasingly possible due to the availability of diverse data sets on ecosystem components and satellite and aircraft-collected high-resolution data that allow for potential driver variables to be quantified at multiple spatial scales. We suggest that the use of CSI power analyses will not only help ecologists design large-scale studies aimed at detecting CSIs, but will also focus attention on explicitly considering ecologically relevant CSI effect sizes—what an ecologically relevant effect size is for any given system and the ability to detect the effect with some level of confidence. Such studies are only possible through the creation and integration of varied data sources, with data quantified at multiple spatial extents, which is challenging and labor-intensive (Soranno et al. 2015). Because CSIs are likely important for extrapolation and scaling up local-scaled results to continental and global-scaled inferences, such integration efforts and power analyses will become increasingly important for future continental- and global-scaled analyses of ecosystem change.

Acknowledgments

Any use of trade, firm, or product names is for descriptive purposes only and does not imply endorsement by the U.S. Government. This is GLERL contribution number 1815. This study was supported by the U.S. National Science Foundation MacroSystems Biology Program in the Biological Sciences Directorate (EF-1065786, EF-1065649, and EF-1065818). TW came up with the idea for the manuscript and led the effort. All authors contributed to refining the question and interpreting the results. TW performed all statistical analyses. TW wrote the first draft of all sections of the manuscript except for the introduction, which was written by CEF. All authors conducted reviews of the MS drafts and approved the final version.

Literature Cited

Bates, D., M. Maechler, B. Bolker, and S. Walker. 2014. lme4: linear mixed-effects models using Eigen and S4. R package version 1.1-7. http://CRAN.R-project.org/package=lme4

Becknell, J. M., et al. 2015. Assessing interactions among changing climate, management, and disturbance in forests: a macrosystems approach. BioScience 65:263–274.

Cash, D. W., W. N. Adger, F. Berkes, P. Garden, L. Lebel, P. Olsson, L. Pritchard, and O. Young. 2006. Scale and cross-scale dynamics: governance and information in a multilevel world. Ecology and Society 11:8. http://www.ecologyandsociety.org/vol11/iss2/art8/

Cheruvelil, K. S., P. A. Soranno, M. T. Bremigan, and K. E. Webster. 2013. The multi-scaled drivers of ecosystem state: quantifying the importance of the regional spatial scale. Ecological Applications 23:1603–1618.

DeWeber, J. T., and T. Wagner. 2015. Predicting brook trout occurrence in stream reaches throughout their native range in the eastern United States. Transactions of the American Fisheries Society 144:11–24.

Dixon Hamil, K.-A., B. Iannone III, W. K. Huang, S. Fei, and H. Zhang. 2016. Cross-scale contradictions in ecological relationships. Landscape Ecology 31:7–18.

Falk, D. A., C. Miller, D. McKenzie, and A. E. Black. 2007. Cross-scale analysis of fire regimes. Ecosystems 10:809–823.

Fergus C. E., P. A. Soranno, K. S. Cheruvelil, and M. T. Bremigan. 2011. Multi-scale landscape and wetland drivers of lake total phosphorus and water color. Limnology and Oceanography 56:2127–2146.

Filstrup, C. T., T. Wagner, P. A. Soranno, E. H. Stanley, C. A. Stow, K. E. Webster, and J. A. Downing. 2014. Regional variability among nonlinear chlorophyll-phosphorus relationships in lakes. Limnology and Oceanography 59:1691–1703.

Fry, J., G. Xian, S. Jin, J. Dewitz, C. Homer, L. Yang, C. Barnes, N. Herold, and J. Wickham. 2011. Completion of the 2006 National Land Cover Database for the Conterminous United States. Photogrammetric Engineering and Remote Sensing 77:858–864.

Gelman, A., and J. Hill. 2007. Data analysis using regression and multilevel/hierarchical models. Cambridge, New York, New York, USA.

Heffernan, J. B., et al. 2014. Macrosystems ecology: understanding ecological pattern and process at continental scales. Frontiers in Ecology and the Environment 12:5–14.

Keane, R. E., D. McKenzie, D. A. Falk, E. A. H. Smithwick, C. Miller, and L.-K. B. Kellogg. 2015. Representing climate, disturbance, and vegetation interactions with landscape models. Ecological Modelling 309–310:33–47.

Koo, K. A., B. C. Patten, R. O. Teskey, and I. F. Creed. 2014. Climate change effects on red spruce decline mitigated by reduction in air pollution within its shrinking habitat range. Ecological Modelling 293:81–90.

Levin, S. A. 1992. The problem of pattern and scale in ecology. Ecology 73:1943–1967.

Mathieu, J. E., H. Aguinis, S. A. Culpepper, and G. Chen. 2012. Understanding and estimating the power to detect cross-level interactions effects in multilevel modeling. Journal of Applied Psychology 97:951–966.

Menge, B. A., T. C. Gouhier, S. D. Hacker, F. Chan, and K. Nielsen. 2015. Are meta-ecosystems organized hierarchically? A model and test in rocky intertidal habitats. Ecological Monographs 85:213–233.

Nash, K. L., et al. 2014. Discontinuities, cross-scale patterns, and the organization of ecosystems. Ecology 95:654–667.

Peterman, R. M. 1990. Statistical power analysis can improve fisheries research and management. Canadian Journal of Fisheries and Aquatic Sciences 47:2–15.

Peters, D. P. C., B. T. Bestelmeyer, and M. C. Turner. 2007. Cross-scale interactions and changing pattern-process relationships: consequences for system dynamics. Ecosystems 10:790–796.

Peters, D. P. C., R. A. Pielke Sr., B. T. Bestelmeyer, C. D. Allen, S. M. Munson-McGee, and K. M. Havstad. 2004. Cross-scale interactions, nonlinearities, and forecasting catastrophic events. Proceedings of the National Academy of Sciences USA 101:15130–15135.

R Core Team. 2015. R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. https://www.R-project.org/

Scherbaum, C. A., and J. M. Ferreter. 2009. Estimating statistical power and required sample sizes for organizational research using multilevel modeling. Organizational Research Methods 12:347–367.

Seaber, P. R., F. P. Kapinos, and G. L. Knapp. 1987. Hydrologic unit maps. U.S. Geological Survey Water-Supply Paper 2294. United States Department of the Interior, Geological Survey, Denver, Colorado, USA.

Snijders, T. A. B., and R. J. Bosker. 1993. Standard errors and sample sizes for two-level research. Journal of Educational Statistics 18:237–259.

Soranno, P. A., et al. 2014. Cross-scale interactions: a conceptual framework for understanding multi-scaled cause-effect relationships in macrosystems.

Frontiers in Ecology and the Environment 12: 65–73.

Soranno, P. A., et al. 2015. Building a multi-scaled geospatial temporal ecology database from disparate data sources: fostering open science and data reuse. GigaScience 4:28.

Steidl, R. J., J. P. Hayes, and E. Schauber. 1997. Statistical power analysis in wildlife research. Journal of Wildlife Management 61:270–279.

Stoffels, R. J., K. R. Clarke, and G. P. Closs. 2005. Spatial scale and benthic community organisation in the littoral zones of large oligotrophic lakes: potential for cross-scale interactions. Freshwater Biology 50:1131–1145.

Vergara, P. M., and J. J. Armesto. 2009. Responses of Chilean forest birds to anthropogenic habitat fragmentation across spatial scales. Landscape Ecology 24:25–38.

Wagner, T., J. R. Bence, M. T. Bremigan, D. B. Hayes, and M. J. Wilberg. 2007. Regional trends in fish mean length at age: components of variance and the power to detect trends. Canadian Journal of Fisheries and Aquatic Sciences 64:968–978.

Wagner, T., P. A. Soranno, K. E. Webster, and K. Spence Cheruvelil. 2011. Landscape drivers of regional variation in the relationship between total phosphorus and chlorophyll in lakes. Freshwater Biology 56:1811–1824.

Supporting Information

Additional Supporting Information may be found online at: http://onlinelibrary.wiley.com/doi/10.1002/ecs2.1417/supinfo