Using Landscape Limnology to Classify Freshwater Ecosystems for Multi-ecosystem Management and Conservation

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Governmental entities are responsible for managing and conserving large numbers of lake, river, and wetland ecosystems that can be addressed only rarely on a case-by-case basis. We present a system for predictive classification modeling, grounded in the theoretical foundation of landscape limnology, that creates a tractable number of ecosystem classes to which management actions may be tailored. We demonstrate our system by applying two types of predictive classification modeling approaches to develop nutrient criteria for eutrophication management in 1998 north temperate lakes. Our predictive classification system promotes the effective management of multiple ecosystems across broad geographic scales by explicitly connecting management and conservation goals to the classification modeling approach, considering multiple spatial scales as drivers of ecosystem dynamics, and acknowledging the hierarchical structure of freshwater ecosystems. Such a system is critical for adaptive management of complex mosaics of freshwater ecosystems and for balancing competing needs for ecosystem services in a changing world.

Keywords: predictive classification, landscape limnology, modeling, ecosystem management, conservation

Many of the underlying principles of ecosystem management have been developed for and applied to charismatic aquatic ecosystems, such as the Florida Everglades, Chesapeake Bay, and Columbia River (e.g., Lee 1993, Gunderson and Holling 2002). These high-profile case studies have generated holistic frameworks for integrating multiple ecological and social drivers and diverse social values to manage more adaptively. Such comprehensive management strategies, although based on sound principles, are difficult to practically apply: The responsible organizations must manage landscapes composed of hundreds to thousands of individual ecosystems (e.g., lakes, streams, or wetlands), often with minimal site-level data. Sparse resources limit the data collection and planning needed to customize management activities to individual ecosystems. Consequently, ecosystems are often treated as if they were all the same, despite evidence that one-size-fits-all policies can cause declines in ecological and social resilience (Carpenter and Brock 2004). Because devising individual management strategies is often impractical, an intermediate approach is to classify ecosystems into a more tractable number of management-relevant classes. This approach is based on the assumption that, within classes, ecosystems will respond similarly to management actions. By classifying ecosystems, management and conservation can be tailored to a much smaller number of situations.

The idea of freshwater ecosystem classification is not new, and various classification approaches have been developed for lakes, streams, and wetlands (e.g., Brinkhurst 1974, Shuter et al. 1998, Euliss et al. 2004). Nevertheless, the integration of classification models into ecosystem management and conservation faces two challenges. First, ecosystem classification fell out of favor with ecologists during the mid-20th century (Elster 1974), perhaps because of its early descriptive nature. For example, early classification models for lake ecosystems, such as those developed by Theinemann and Naumann during the 1920s, classified lakes on the basis of their overall productivity (Rodhe 1975). This type of classification model, in which a variable of interest classifies the ecosystem, is not based on causal relationships and is of limited use for prediction. In contrast, "predictive" classification models are those that use one or more variables to classify ecosystems based on causal relationships with the variable of interest (Brinkhurst 1974). We focus the rest of our discussion on these predictive classification models, which we suggest have been insufficiently studied by ecologists and underused by ecosystem managers and conservationists.

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The second challenge for ecosystem classification modeling has been the lack of an explicit link between the type of predictive classification model used (and its associated end point) and the management or conservation goal. Managers and decisionmakers have many goals that fall into one of six general categories (table 1); the best classification model will depend strongly on the specific goal and the desired end point for the model. For example, if we are interested in setting restoration targets for nutrient concentrations in a population of streams (goal 2, table 1), we could use a predictive classification model to group together streams with similar nutrient concentrations in the absence of human impacts (i.e., the "reference" nutrient concentration). Such classes would be characterized by "homogeneous states in the response variable" (i.e., nutrient concentrations). An important assumption underlying many such classification models is that ecosystems within such homogeneous classes respond similarly to stressors such as catchment land use; however, this assumption is rarely evaluated and may not be valid. Alternatively, if we want streams grouped into classes such that they respond to stressors similarly (e.g., land use; goal 4, table 1), it is better to group streams by "homogeneous responses to stressors" (i.e., similar functional relationships between stream nutrients and land use). These examples highlight the need to choose a predictive classification model that explicitly meets the management or conservation goal before one begins classification model development.

Although it is possible for a single classification model to meet multiple goals, this is unlikely (Hawkins et al. 2000, Mac Nally et al. 2002). Therefore, we need a system within which we can develop multiple classification models, each meeting some subset of specific objectives. Here we present such a predictive classification modeling system for freshwater ecosystems that includes the key elements necessary for effective management and conservation of any large group of ecosystems (figure 1). Our classification system has two important features. First, it is designed with the flexibility to address any of the six categories of ecosystem management and conservation goals through the inclusion of options for developing state-based or response-based predictive classification models (table 1). Second, it has a foundation in landscape limnology (box 1), which addresses the underlying spatial complexity of freshwater ecosystems across the landscape, including hierarchical processes that operate at multiple spatial scales.

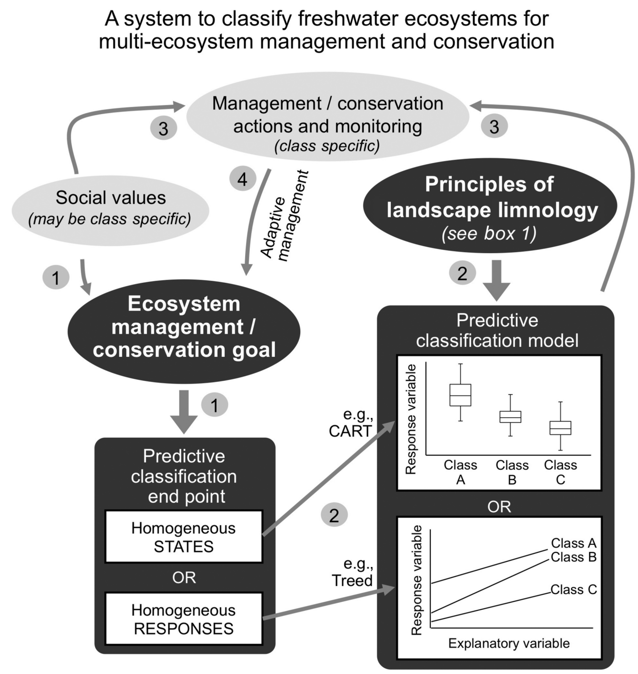


Figure 1. Overview of our system to classify freshwater ecosystems for multi-ecosystem management and conservation. The dark gray ovals and rectangles represent the unique components of our approach that explicitly link the ecosystem management or conservation goal to the predictive classification end point (step 1), and that explicitly link the principles of landscape limnology with predictive classification modeling (step 2). The lighter gray ovals represent additional considerations to be included in our approach for a more integrated ecosystem management system. CART, classification and regression tree analysis.

Table 1. Common management and conservation goals and end points best suited for landscape-scale management and conservation of ecosystems.

Goal	Example	Predictive classification model end point
Assess status	Conduct surveys to quantify ecosystem characteristics (i.e., physical, chemical, and biological features).	Homogeneous states
Set restoration or rehabilitation targets	Choose a minimally disturbed restoration goal using available data (e.g., nutrient levels, biological assemblages).	Homogeneous states or responses
Conserve biota and habitat	Identify ecosystems of special interest with regard to rare or endangered biota or habitats, or overall biodiversity.	Homogeneous states
Quantify response to stressors	Determine relationships between response variables and human activities.	Homogeneous responses
Detect temporal trends	Determine temporal responses to mitigation actions.	Homogeneous states or responses
Set policy	Designate standards for ecological integrity or human use.	Homogeneous states or responses

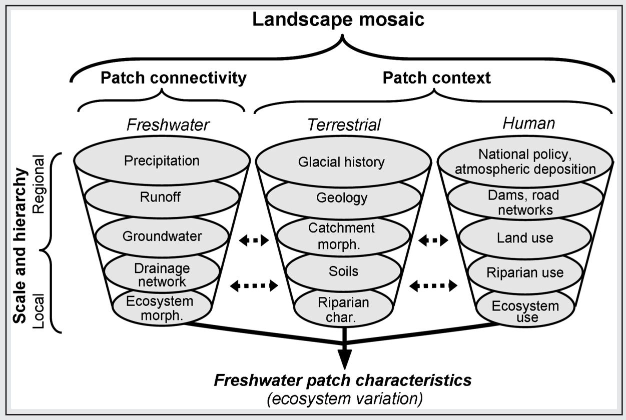
Box 1. Defining landscape limnology.

Landscape limnology is the spatially explicit study of lakes, streams, and wetlands as they interact with freshwater, terrestrial, and human landscapes to determine the effects of pattern on ecosystem processes across temporal and spatial scales.

Principles of landscape limnology

The core principles of landscape ecology and, in particular, the patch-mosaic model of landscapes, provide the foundation for landscape limnology. We begin with the same premise that Wiens (2002) does—that rivers can be considered patches—but we extend this idea to include all freshwater components (rivers, lakes, wetlands, and groundwater), which we define as the freshwater landscape. This landscape is embedded in a terrestrial and human mosaic that can be considered either as discrete patches or continuous gradients, depending on the processes one considers and the scale at which they operate (McGarigal and Cushman 2005). We present four main principles of landscape limnology for defining and studying freshwater ecosystem patches.

1. *Patch characteristics*: The physical, chemical, and biological features of a freshwater ecosystem.
2. *Patch context*: Freshwater ecosystems are embedded in a complex mosaic of terrestrial and human features (e.g., geology and land use) that drive many freshwater processes such as water chemistry, species richness, and primary productivity. Freshwater patch boundaries (e.g., riparian zones), in particular, are often a focal point for important ecosystem processes linking freshwater, terrestrial, and human landscapes.
3. *Patch connectivity and directionality*: The freshwater landscape defines corridors and regions that allow for the movement of materials and organisms among lakes, streams, and wetlands. These connections often display a strong directionality that must be explicitly considered.
4. *Spatial scale and hierarchy*: Hierarchy is important in landscape limnology because (a) many freshwater ecosystems and their landscapes are hierarchically organized and controlled by processes that are hierarchically organized; (b) most freshwater ecosystems are managed at multiple spatial scales, from policy set at the national level to land management conducted at local scales; and (c) the degree of homogeneity among freshwater ecosystems can change in relation to the scale of observation.



Landscape limnology framework. *Freshwater ecosystems vary in their patch characteristics (an individual lake, stream, or wetland). These characteristics (abbreviated char in the figure) are a function of patch context, which is defined by the terrestrial and human landscapes, and by patch connectivity, which is defined by the freshwater landscape. "Spatial scale and hierarchy" must be considered within each of the three major landscape types. The ovals in the figure are organized hierarchically and are examples of the features within each landscape that are important drivers of freshwater ecosystem variation. The specific landscape variables used in a given modeling effort will be particular to the management goal, the response variable, the hypothesized relationships between landscape predictors and ecosystem responses, and the freshwater ecosystem type under consideration. Source: Modified from Soranno and colleagues (2009). Catchment morphometry (morph, in the figure) refers to catchment size or relief.*

Our goal is to describe and demonstrate the use of our predictive classification system and discuss its implications. First, we explain the general features of the system, including the theoretical foundation of landscape limnology upon which it is based. Second, we present an application of our classification system that highlights two alternative modeling approaches using a data set containing 1998 freshwater lakes. Although we use lakes in our example, our approach can be applied to any group of discrete ecosystems that must be managed or conserved at broad spatial scales. In addition, the modeling step is flexible enough that it can include any type of model that results in discrete classes of ecosystems (e.g., Cutler et al. 2007). Third, we discuss support for our approach from the literature. Finally, we outline ways to move the science of predictive ecosystem classification modeling forward, and consider challenges and opportunities associated with multi-ecosystem management and conservation.

A system to classify freshwater ecosystems for multi-ecosystem management and conservation

Our system directly addresses challenges faced by the agencies and organizations that use minimal site-specific data to manage and conserve multiple ecosystems. There are four main steps, numbered in figure 1, that make up our system:

1. Choose the predictive classification end point of either homogeneous states or homogeneous responses based on the ecosystem management or conservation goal (informed by social values). If possible, the goal should be stated quantitatively to allow for explicit measurement of the response to management actions (Tear et al. 2005).
2. Create ecosystem classes containing either homogeneous states or responses from a predictive classification model based on landscape limnology principles (see box 1). Choose predictor variables in the model from those known or hypothesized to have functional relationships with the response variable.

3. For each class, develop management actions in concert with class-specific social values and monitor a subset of the ecosystems within each class.
4. Evaluate the management actions using the monitoring data, revisit the management or conservation goal and associated social values (Trexler and Busch 2003), and refine the predictive classification models by including new data to reduce prediction error.

The focus on continual monitoring and revision of the classification models also allows for repeated examination of potentially changing social values. We suggest that this cycle represents one component of an overall adaptive management strategy that would also include other adaptive approaches focused on learning through experimentation and monitoring, despite the challenges that have been identified (Walters 2007).

Our classification system has its foundation in the principles of landscape ecology developed for freshwater ecosystems, which we call "landscape limnology" (box 1). To integrate the disparate efforts of ecologists working in streams, wetlands, and lakes, we retain the original definition of limnology as a science that is inclusive of all inland aquatic ecosystems, not just lakes (Elster 1974). Others have recognized the importance of integrating landscape ecology concepts and methods into studies of rivers (Pringle et al. 1998, Fausch et al. 2002, Poole 2002, Wiens 2002), lakes (Magnuson and Kratz 2000, Soranno et al. 2009), and wetlands (Wang et al. 2008, Bouvier et al. 2009). However, to date, the most common applications of landscape ecology to freshwater research have been the identification of spatially explicit relationships between land and a particular type of freshwater ecosystem. Less frequently considered are water-to-water relationships, or those relationships that incorporate multiple types of freshwater ecosystems in addition to the terrestrial landscape. This tendency to focus on individual freshwater ecosystem types and on primarily land-water interactions is changing with the more recent emphasis on freshwater ecosystems that are spatially structured and that interact strongly with each other as well as the surrounding landscape (Winter 2001, Cardille et al. 2007, Dahl et al. 2007, Milner et al. 2007). Thus, it makes sense to have a more comprehensive, flexible perspective that explicitly incorporates the effects of different freshwater ecosystem types on each other. Although we recommend that each freshwater ecosystem type should have its own classification system, the core features of the system and the underlying landscape limnology principles are the same for all freshwater ecosystems (see box 1).

In general, any broadscale ecosystem management system must be based on data that are available for all ecosystems, that span multiple spatial scales, and that are able to predict at least some aspect of the management variable of interest. The wide range of available geospatial data sets for freshwater, terrestrial, and human landscape features meets these criteria (Johnson and Gage 1997). In fact, advances in spatial technology and remote sensing continue to provide increasingly more detailed databases on key predictors such as land use and land cover, soils, imperviousness, and spatial configuration of freshwater ecosystems. To build predictive classification models, we also need within-ecosystem response data collected from a wide range of ecosystems that are representative of the population of ecosystems to be managed. National, state, or regional agencies typically perform periodic surveys of freshwaters that meet this criterion.

Spatial scale is important to consider when managing multiple ecosystems across large spatial extents, particularly the idea that finer-scaled (i.e., subregional) features are constrained by broader-scaled (i.e., regional) features, such as climate and geology. Such broadscale landscape features are often accounted for in predictive classification modeling by including a regionalization framework made up of spatial units such as major river watersheds or ecoregions (e.g., Wickham et al. 2005). Most regionalization frameworks use factors such as geology, landform, and climate to divide landscapes into discrete homogeneous spatial units that are composite variables representing a mix of geographic features (e.g., Bailey 1983). The assumption underlying their use is that these regional composite features explain freshwater ecosystem heterogeneity. However, recent research has shown that ecoregions alone have limited ability to explain homogeneous states in water chemistry (e.g., Hawkins et al. 2000, Cheruvelil et al. 2008). Thus, hierarchical approaches such as the one we propose here are needed to successfully capture variation due to both regional and subregional processes (Hawkins et al. 2000).

Application of the predictive classification system to north temperate lakes

Next we provide an example application of steps 1–3 of our system (figure 1) to illustrate the importance of explicitly linking the management goal of interest—here, the setting of restoration targets related to eutrophication for 1998 north temperate lakes—with the predictive classification model used. Our example falls within the broader ecosystem management goal of setting restoration targets (goal 2 in table 1), for which either a state-based or response-based approach can be most appropriate (i.e., homogeneous ecosystem states or homogeneous ecosystem responses, respectively), depending on the specific needs of the agency managing the lakes.

Background on approaches used to develop nutrient criteria. For setting restoration targets related to lake eutrophication, we draw upon guidance for developing nutrient criteria provided by the US Environmental Protection Agency (EPA) (USEPA 2000). Generally, nutrient criteria are intended to be measurable indicators that determine whether water bodies are meeting designated uses as mandated by the US Clean Water Act. Nutrient criteria are designed to minimize the undesirable symptoms of eutrophication, typically defined as excess algal biomass measured by the concentration of chlorophyll (Chl) in water. Total phosphorus (TP) concentrations in water are usually used as a criterion because phosphorus is most often the nutrient that limits algal growth, and it has a well-established positive relationship with Chl.

One approach for developing lake nutrient criteria that the EPA has proposed is state based; observed TP concentrations from minimally disturbed reference lakes are adopted as the target for all lakes within an ecoregion (USEPA 2000). Because this approach requires a sufficiently large number of reference lakes, it is untenable in ecoregions with widespread human disturbance. In such cases, the EPA has suggested an alternative state-based approach that uses an arbitrary cutoff, such as the 25th percentile of lake TP concentrations in an ecoregion, as the target. This approach is suitable if TP data are available from a random subset of lakes, and if the percentage of lakes above minimum impact levels is known; the 25th percentile is most appropriate where 75% of the lakes exceed minimal impact levels. However, in practice, both of these conditions are rarely met (Herlihy and Sifneos 2008).

Interestingly, both of these state-based approaches for setting nutrient criteria assume that within a given ecoregion, the Chl concentration in lakes will respond in the same way to decreases or increases in lake TP. Because the state-based approaches described above do not explicitly account for potential differences in the relationship between TP and Chl, Reckhow and colleagues (2005) advised that nutrient criteria based on response-based relationships provide better guidance to achieve management objectives. Soranno and colleagues (2008) presented a regression approach that incorporates response-based relationships to set nutrient criteria within a landscape-based predictive modeling framework. In the example application here, we compare predictive classification modeling approaches representing both state-based and response-based approaches to setting nutrient criteria.

Lake and landscape data. We used a 1998-lake data set from a six-state region in the midwestern and northeastern regions of the United States (figure 2; see Webster et al. 2008 and Soranno et al. 2009 for database details). We obtained TP and Chl concentrations, lake depths, and lake catchment areas from the state agencies responsible for monitoring lakes under the US Clean Water Act, which requires standard procedures and quality assurance and quality control protocols. Concentrations of TP and Chl were measured in water collected from the mixed surface layer during the summer-stratified period (July–September). We used single observations for each lake, sampled predominantly between 1990 and 2003.

We included landscape predictor variables from the three main landscapes (freshwater, terrestrial, and human) that influence freshwater ecosystems (described generally in box 1 and specifically for this analysis in table 2). We used

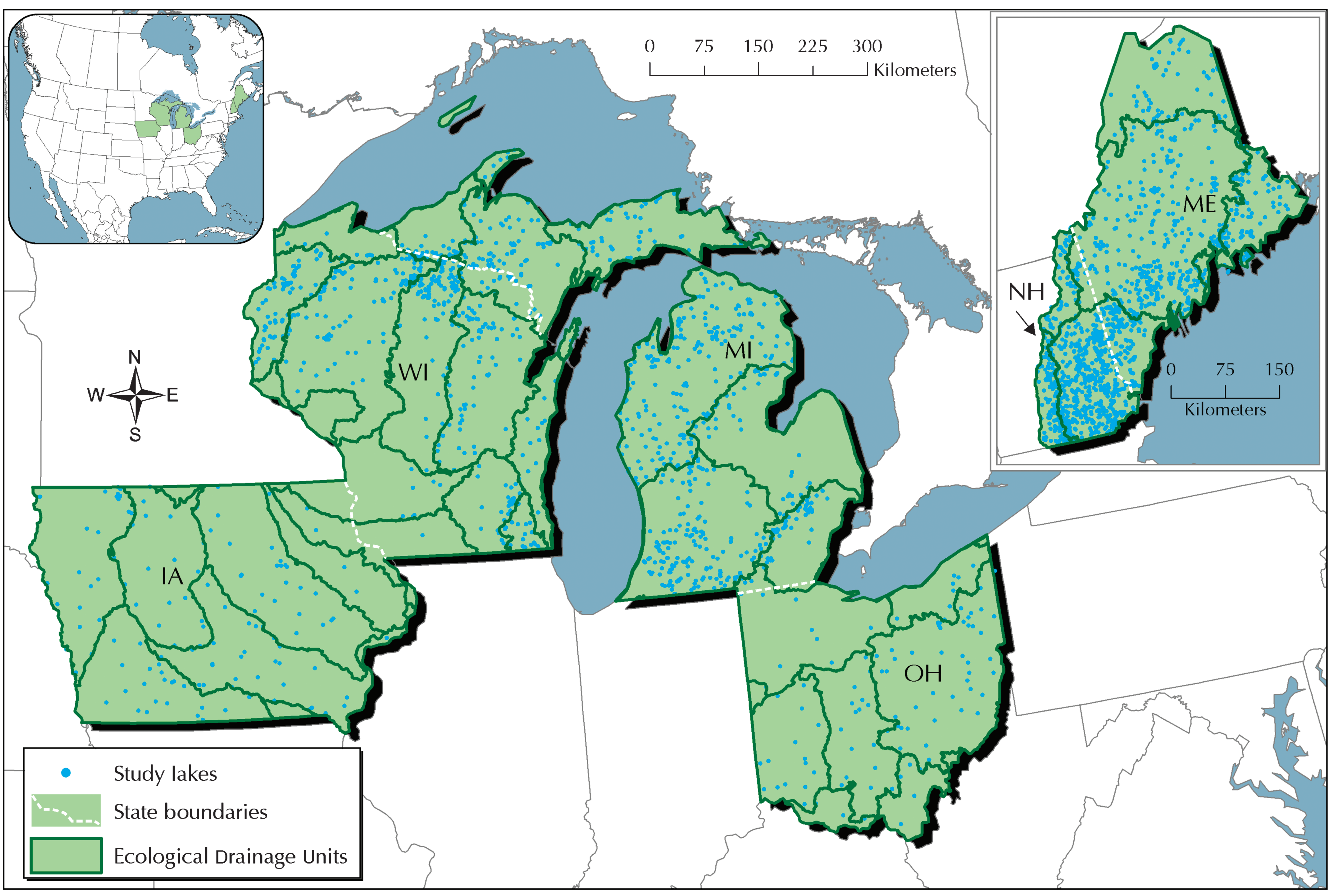


Figure 2. Map of the study region showing the study lakes, the state boundaries, and the ecoregion boundaries (Ecological Drainage Units; Higgins et al. 2005).

Ecological Drainage Units (EDU, hereafter, ecoregions; Higgins et al. 2005) as our regionalization framework. These ecoregions have boundaries set by river watersheds (thus incorporating a coarse measure of freshwater connectivity) that are then agglomerated on the basis of physiography and climate; therefore, the EDU delineation includes both freshwater and terrestrial landscape components (box 1). At subregional scales, we included landscape variables that reflect the freshwater landscape (e.g., lake depth, percentage of wetland cover, baseflow, runoff, and precipitation), terrestrial landscape (e.g., forest cover, catchment morphometry, and quaternary sediment thickness), and human landscape (human land use and land cover, road density, and human population variables from the 1990 US census data set). We obtained climate, land use, and geology variables from federal agency data sets available at the national scale.

Statistical approaches for predictive ecosystem classification. We performed three classifications, all with the goal of setting restoration targets for lake eutrophication: classifying lakes by TP, classifying lakes by Chl, and classifying lakes by the response of Chl to TP. The first two classifications correspond to state-based goals for which managers identify the characteristics of lakes that exceed thresholds for TP or Chl. The third classification corresponds to a response-based goal for which a manager determines class-specific responses of Chl to TP in order to identify the appropriate level of TP concentration necessary to achieve an acceptable level of algal biomass (as measured by Chl).

We used two different predictive modeling approaches for the three classifications. First, state-based classification and regression tree (CART) models create classes with homogeneous states with a narrow range of values optimizing the variation around the mean. Second, response-based Bayesian treed models create classes with homogeneous responses with a wide range in the predictor and response variables and they optimize the parameters of linear regressions. For the state-based models, we created two classifications (one for TP and one for Chl) using CART models in the R software system using the rpart library (RDCT 2008, *www.r-project.org*). The CART procedure operates by recursively partitioning the data set into subsets that are increasingly homogenous with respect to the response variable (Breiman et al. 1984); each level or split is defined by the value of a particular predictor variable. For the response-based model, we identified classes of lakes with homogeneous relationships between ln(Chl) and ln(TP) using Bayesian treed models (Lamon and Stow 2004) with software developed by Chipman and colleagues (2002). Treed models are a variation on the CART model, in which the end nodes are simple linear regression models instead of classes with similar means. The Bayesian treed algorithm, guided by prior distributions, searches stochastically for good classification trees (Chipman et al. 2002). Both classification model approaches create predictor-tree diagrams that show which landscape predictor variables partition the data to produce homogeneous class means (CART) or responses (treed).

To compare these three classifications, we conducted statistical analyses that are commonly used to compare classes formed by ecosystem classification. We used analysis of variance (ANOVA) to compare class means (as per state-based approaches for either TP or Chl). To compare the functional relationship between TP and Chl, we used Chl as the response and TP as the predictor variable in (1) univariate regressions for each individual lake class; and (2) mixed model regressions that allow the intercept,

Table 2. Landscape variables (ordered approximately from regional scale [top] to local scale [bottom] within each column) used to develop the predictive classification models in the example application.

Freshwater landscape	Terrestrial landscape	Human landscape
Ecoregion (Ecological Drainage Unit)	Ecoregion (Ecological Drainage Unit)	Population density
Mean precipitation (1971–2000)	Quaternary sediment characteristics and thickness	Housing density
Mean runoff (1951–1980)	Catchment area	Road density
Mean baseflow index of streams near lake	Ratio of catchment area to lake area	Percentage pasture agriculture
Water residence time index	Percentage forest cover	Percentage row crop agriculture
Percentage open water	Lake elevation	Percentage urban
Percentage wetland cover		Percentage households with income > $100,000
Lake depth, mean		Median number of rooms in housing units
Lake depth, maximum		Percentage housing units with septic sewage disposal
		Percentage housing units built before 1940
		Percentage housing units built between 1980 and 1989

Note: Ecoregion is included in both the freshwater and terrestrial landscape categories because this framework considers major river watersheds in its delineation of regions in addition to climate and landform. Most variables were quantified for the 500-meter equidistant buffer around each lake, an index of the local lake catchment, except for the human population variables, which were quantified at the county subdivision scale.

slope, and residual variance to vary among lake classes. The mixed-model regression approach allowed us to compare lake classes by factoring in all class-specific regressions simultaneously for each classification. We used Akaike's information criterion (AIC) to compare the mixed models from the three classifications. We include statistics on classification models for which the models were not intended (e.g., we show ANOVA results for the response-based treed models) for comparison purposes only; researchers and managers can make the mistake of conducting analyses on classes for which the modeling approach was not intended, and we want to emphasize the importance of linking the management goal with the statistical approach.

Interpreting predictive classification models. The three modeling approaches resulted in different classifications (i.e., lakes with different class membership) producing three and seven classes for the Chl and TP CART models, respectively (figure 3), and three classes for the treed model (figure 4). All classifications were defined by regional landscape predictor variables (ecoregion and runoff), and in some cases, subregional predictor variables (figures 5, 6; lake depth and agricultural land use). Statistics for all three models are summarized in table 3.

To examine the relevance of a classification, we must look beyond statistical fit and significance and consider the ecological implications of the results. For example, although the TP state-based model included two classes (P3 and P4) with very similar means and ranges of TP (figure 3), the predictor-tree diagram (figure 5a) shows that the landscape predictor variables that formed these two classes differed, suggesting differences in the underlying causes of the similar TP concentrations in the two classes. Lakes in the P3 class were deep and had pasture agriculture exceeding 3.7% of their catchment area, whereas lakes in the P4 class were shallow. This result is consistent with known causes of elevated TP concentrations in lakes: Shallow lakes generally have higher TP than deeper lakes as a result of internal loading, whereas lakes with higher percentage agriculture in their catchments generally have higher TP as a result of the export of nutrients from agricultural activities. If we were to classify lakes using only TP concentrations, without including

Table 3. For each classification modeling approach, we compare two statistical analyses that are commonly conducted on ecosystem classifications: ANOVA (analysis of variance) and univariate regression.

		Homogeneous states		Homogeneous responses				
		ANOVA		Regression				
Classes	Number of lakes per group (n)	Total phosphorus (TP) r^2	Chlorophyll (Chl) r^2	r^2	Mean square error	Intercept	Slope	Mixed-model AIC[a]
CART: TP classes								
P1	293	**0.54**	**0.36**	*0.06*	*0.67*	*0.43*	*1.27*	*4329*
P2	439			*0.11*	*0.61*	*0.49*	*0.38*	
P3	178			*0.23*	*0.81*	*−0.58*	*0.77*	
P4	701			*0.19*	*0.75*	*0.09*	*0.59*	
P5	240			*0.61*	*0.68*	*−1.45*	*1.10*	
P6	49			*0.31*	*0.79*	*−0.44*	*0.91*	
P7	98			*0.23*	*0.75*	*0.74*	*0.63*	
CART: Chl classes								
C1	430	**0.37**	**0.34**	0.09	0.70	0.34	0.32	*4319*
C2	1397			0.32	0.70	−0.08	0.66	
C3	171			0.41	0.76	0.17	0.76	
Treed: Response classes								
T1	274	*0.33*	*0.21*	**0.60**	**0.74**	**−0.86**	**0.97**	**4268**
T2	521			**0.39**	**0.83**	**−0.81**	**0.80**	
T3	1203			**0.33**	**0.64**	**−0.002**	**0.66**	

Note: Analyses that are statistically appropriate for the classification approach used to create the classes are shown in bold: ANOVA for CART models, and regression and mixed model for treed models. Analyses that are statistically inappropriate for the classification approach used to create the classes are shown in italics and for comparison purposes only. r^2, mean square error, intercept, and slope are for the linear regression between ln(Chl) and ln(TP) in each class.

a. We fit a linear mixed regression model using ln(Chl) as the response and ln(TP) as the predictor variable, and allowed the intercept, slope, and residual variance to vary among lake classes. We used Akaike's information criterion (AIC) to compare the classification models. The classification model with the lowest AIC value compared to the others (> 7 units difference) has the best functional relationships between TP and Chl within each of its lake classes.

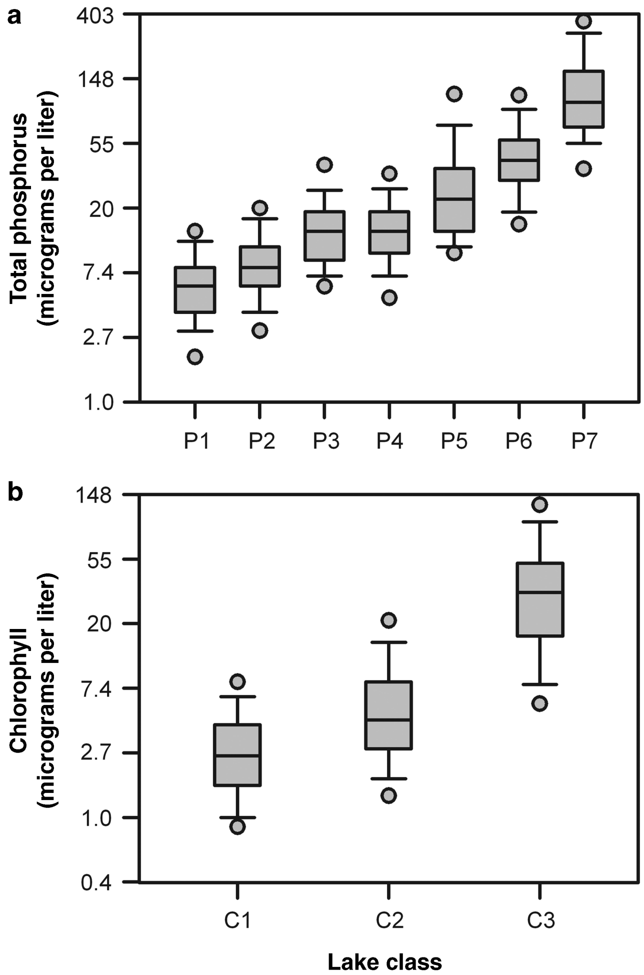


Figure 3. Box plots of (a) total phosphorus and (b) chlorophyll in micrograms per liter for lake classes identified by fitting classification and regression tree models (CART; class codes correspond to classes in table 3). The y*-axes are plotted on a natural log scale. Box boundaries are the 25th and 75th percentiles, whiskers are the 10th and 90th percentiles, circles are the 5th and 95th percentiles, and the inner horizontal line is the median.*

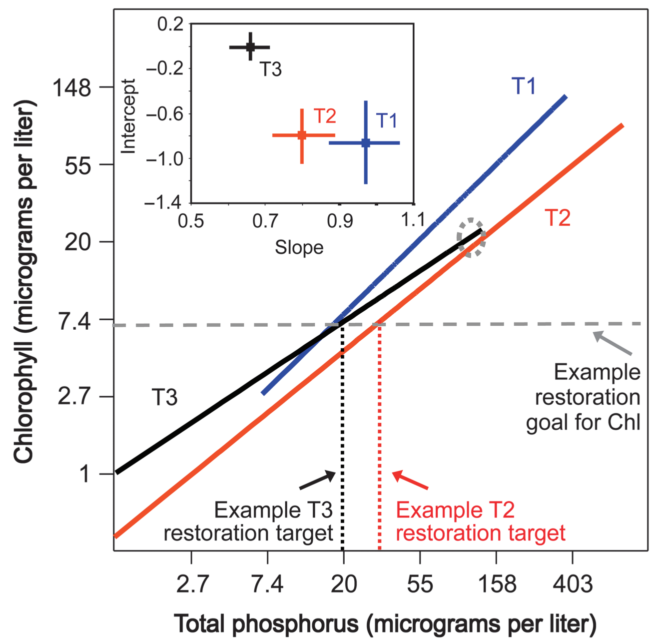


Figure 4. Fitted regression lines for the relationship between natural log total phosphorus (TP) and natural log chlorophyll (Chl) for the three lake classes created by fitting a treed model (class codes correspond to classes in table 3). The x*- and* y*-axes are plotted on a natural log scale. The gray dashed circle refers to the example presented in the text regarding a starting point for a group of lakes to be restored from a Chl concentration of approximately 20 micrograms per liter to a restoration target of approximately 7 micrograms per liter (horizontal gray dashed line). The black and red dashed vertical lines refer to the TP reduction targets to meet the Chl restoration goal for T3 and T2 respectively. Inset: Slopes are plotted against the intercepts for each treed lake class (error bars are the 95% credible intervals).*

predictor variables, we would not have identified these underlying differences related to landscape setting.

As another example, suppose that we set the eutrophication target for Chl in lakes at 7 micrograms (µg) per liter (L) to represent a minimally disturbed restoration goal (table 1). We are managing a group of eutrophic lakes that currently have TP concentrations of about 100 µg per L, and Chl concentrations of about 20 µg per L; we wish to restore these values to levels of Chl around 7 µg per L (figure 4; "example restoration goal"). On the basis of our response-based classification model, these lakes could belong to either class T2 or T3 (i.e., the 95% credible intervals [CI] of the regression lines overlap in this portion of figure 4 [CIs not drawn]). If the lakes belong to class T2, we would set a TP reduction target of 31 µg per L; however, if the lakes belong to class T3, we would set a much lower TP reduction target of 19 µg per L. These alternative values of TP at 7 µg per L Chl are both ecologically and statistically different (i.e., the CIs in this range of the graph do not overlap). Using a predictive classification model, we can correctly identify the lakes' class and set the appropriate TP target to meet the restoration goal of 7 µg per L Chl. Although the criterion we used in this example is arbitrary, it is ecologically plausible, as other studies have set Chl criteria in this general region (Heiskary and Wilson 2008). The differences among models are biologically important because even small increases in TP can lead to increases in the probability of a lake experiencing algal blooms that severely limit the ecosystem services provided by lakes (Heiskary and Wilson 2008). In addition, improved understanding of the functional differences among lake classes can lay the groundwork for analyses that integrate social values into ecosystem management. For example, differences among lake classes can be used to determine where management efforts and resources to reduce TP can be most efficiently applied to achieve the greatest reduction in Chl, thus meeting a social value of cost-effectiveness (figure 1).

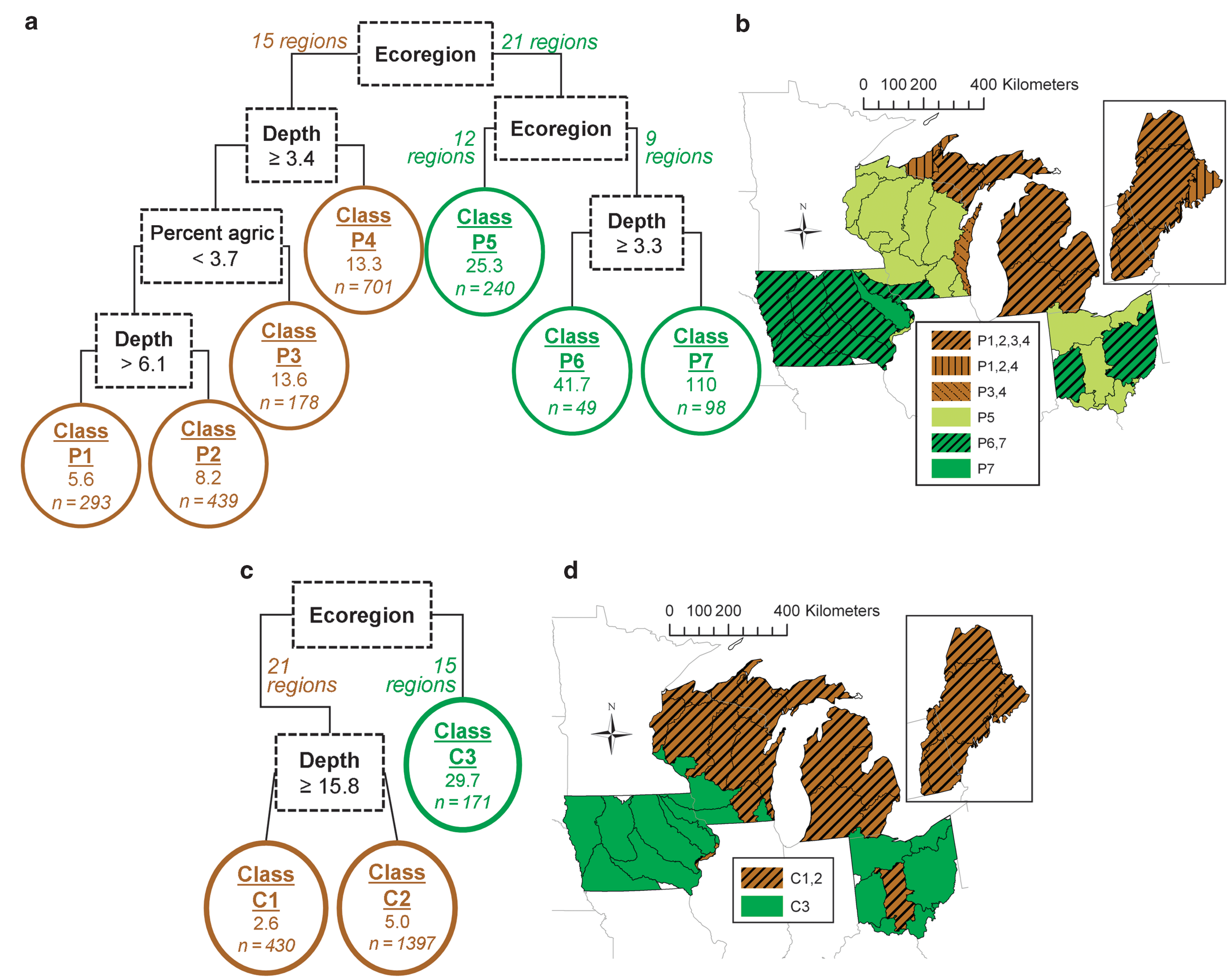


Figure 5. Tree diagrams from the classification and regression tree models (a, c) and maps of the resulting lake classes found within each ecoregion (b, d) using freshwater, terrestrial, and human landscape features as the predictor variables and either total phosphorus (TP; a, b) or chlorophyll (Chl; c, d) as the response variable. For the tree diagrams (a, c), the dashed box indicates the split, containing the name and split value of the predictor variable. The split values define the nodes on the left side of the split. For ecoregion (a categorical variable), the number of ecoregions that are found at each split is provided and shown in the map to the left (see below; color-coded to match the final lake classes in the corresponding tree figure to the right). Solid circles indicate the final lake classes and include the class code (see table 3), the mean TP or Chl concentrations in micrograms per liter, and the number of lakes per class. For the maps (b, d), solid colors are for splits in the CART model defined by ecoregion alone (i.e., all lakes within an ecoregion are in the same lake class), and hatched fills are for ecoregions that contain more than one lake class based on subregional variables. The underlying color of the hatching represents group ecoregion membership as displayed in the predictor trees (a, c). In the map legend, combinations of lake classes are separated by a comma such that P3,4 is for ecoregions that contain lake classes P3 and P4. State boundaries are shown with gray lines and ecoregion boundaries are shown with black lines. Abbreviation: percent agric, percentage pasture agriculture in the 500-meter lake buffer. Depth is mean lake depth in meters.

There are three important take-home messages from our results: (1) the predictive classification modeling approach must be chosen to match the ecosystem management goal, (2) the relative importance of regional versus subregional landscape factors can differ for each predictive classification modeling approach, and (3) predictive ecosystem classification modeling provides an opportunity for improved understanding of freshwater ecosystem variation.

Matching the management goal to the classification modeling approach. Our a priori expectations were that the state-based CART classification model would perform better (as measured by ANOVA) than the response-based treed model for a state-based management goal, and that the response-based treed classification model would perform better (as measured by univariate and mixed-model regressions) for a response-based management goal (table 3). Our analyses

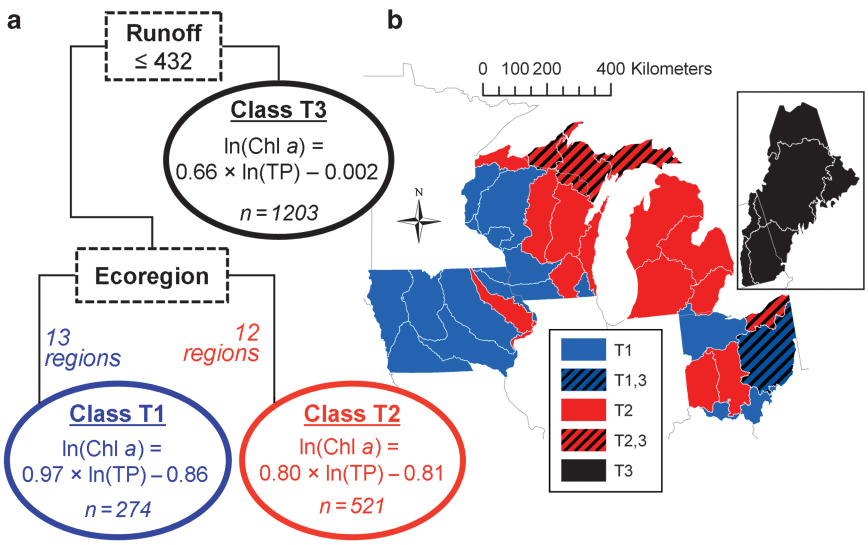


Figure 6. (a) Tree diagram from the treed analysis and (b) a map of the resulting lake classes found within each ecoregion using freshwater, terrestrial, and human landscape features as the predictor variables and the linear regression of natural log chlorophyll (Chl) versus natural log total phosphorus (TP) as the response variable. The tree diagram format is as for figure 5. Solid circles are the final lake classes and include the class code (see table 3), the linear regression model, and the number of lakes per class. Runoff is the mean annual runoff (1951–1980) in millimeters per year in the 500-meter lake buffer. The map format is as for figure 5. In the map legend, combinations of lake classes are separated by a comma such that T1,3 is for ecoregions that contain lake classes T1 and T3. State boundaries are shown with gray lines and ecoregion boundaries are shown with white lines.

supported both expectations. First, the state-based classifications had higher ANOVA r^2 (table 3a, 3b) values than the response-based classifications for both TP and Chl (table 3). Second, the response-based classification had class-specific regressions with $r^2 > 0.30$ as compared with only two of seven class-specific regressions from the state-based models with $r^2 > 0.30$ (table 3). In addition, the TP state-based class that had the highest r^2 (P5 of the TP state-based classification) also had the largest TP interquartile range within a class (figure 3). These results demonstrate that because state-based models are designed to create narrow ranges in the classification variable, they will be of limited use in creating classes for regression analyses.

Finally, the linear mixed-model analysis comparing the fit of all class-specific linear regressions in combination indicated that the response-based model had the lowest AIC, and thus the best performance, confirming our previous analysis (table 3). In sum, if the management goal is state based—for example, identifying the types of lakes that have exceeded a TP criterion—we would recommend using state-based CART classification models; if the goal is response based—such as identifying the types of lakes whose algal biomass (as measured by Chl) responds similarly to changes in TP—we would recommend using the response-based treed classification models.

The relative importance of regional and subregional landscape factors. We found two important results related to the landscape predictor variables. First, regional landscape factors were the first variables included in all classification models (figures 5, 6). This finding suggests that, in studies of large spatial extent that span broad gradients in landscape features, it is important to include regional variables such as ecoregion and runoff (Herlihy and Sifneos 2008). Although the predictive classification models do not explain *why* regional factors are so important for classifying lake TP and Chl, they do highlight this issue as one needing further study.

Second, we found interesting differences in the importance of subregional variables across the classification modeling approaches. Specifically, the state-based classifications of TP and Chl included subregional variables (i.e., any variable that is at a finer scale than regional) of lake depth or percentage of pasture agriculture (figure 5a, 5b), whereas the response-based classification included no subregional variables (figure 6). This result is illustrated in the maps of lake classes by ecoregion (figures 5, 6). For the state-based models of TP and Chl, many of the ecoregions contained more than one lake class (indicated by hatched filling in many ecoregions of figure 5b, 5d). On the other hand, for the response-based models of Chl versus TP, few ecoregions contain more than one lake class (indicated by few ecoregions with hatched filling in figure 6b). These results suggest that although subregional variables may be needed for state-based goals and models, response-based goals and models may be met and built using only regional landscape predictor variables. The generality of this result warrants further study, especially because regional-scale variables are easier to obtain for all ecosystems. There is strong support in the literature for the recognition of the importance of considering spatial scale and hierarchy in freshwater landscapes and for the contention that regional factors alone do not explain homogeneous states (e.g., Tonn 1990, Hawkins et al. 2000, Pyne et al. 2007, Cheruvelil et al. 2008); however, few studies have considered these issues for functional relationships such as the one between Chl and TP.

Using predictive classification modeling to improve understanding. Predictive classification modeling within a landscape limnology framework can point to the underlying mechanisms that determine whether freshwaters behave similarly, and modeling can help identify interesting questions that warrant further study. For example, regional variables emerge as a key factor in predictive classification models of lake nutrients, and we need to understand why. Two key questions are raised by our example application. First, what features of ecoregions influence how lake Chl responds to TP? Second, because ecoregions themselves are often delineated at multiple hierarchical levels, what is the optimal spatial scale with which to define ecoregions for homogeneous responses? Our perspective provides the framework to identify a variety of important ecological questions and generate testable hypotheses, which in turn will lead to greater insights regarding the behavior of freshwater ecosystems in a landscape context.

Support for our freshwater classification system

Ample evidence from the literature indicates that it is unlikely for a single classification model to meet conservation or management goals for multiple response variables such as multiple taxonomic groups (Hawkins et al. 2000, Mac Nally et al. 2002, Vander Zanden and Olden 2008) or multiple water-chemistry variables (Cheruvelil et al. 2008). Our application also showed that even for two closely related variables, different classes were created depending on the management goal end point. This result underscores the importance of the step that links the goal to the predictive classification model end point. At first glance, this suggestion may seem to be an unwieldy solution requiring individual classification models for each management and conservation goal, and each response variable. Rather, we interpret these results as pointing us in the direction of much-needed research that explicitly addresses when a particular classification model can meet multiple goals, and when it cannot (e.g., Mac Nally et al. 2002). The focus thus shifts from identifying one overarching policy to identifying a suite of policies tailored to different ecosystem classes and potentially different social values. However, how does one decide when ecosystems are similar enough to be addressed by the same policy? And how many different policies are needed? These questions can be answered using a formal predictive classification system such as the one we have described.

Our system builds on recent efforts to develop approaches for broadscale biodiversity conservation planning for both terrestrial and freshwater ecosystems (Gutzwiller 2002). For example, researchers and conservation agencies have recognized the need for (a) an explicit statement of goals that are linked to quantifiable objectives (Tear et al. 2005), (b) consideration of multiple spatial scales as drivers of ecosystem dynamics (Poiani et al. 2002, Higgins et al. 2005), (c) consideration of the hierarchical organization of freshwater ecosystems (Poiani et al. 2002, Higgins et al. 2005), (d) a foundation of mappable data that are available for all ecosystems (Groves et al. 2002, Poiani et al. 2002, Dietz and Czech 2005, Higgins et al. 2005), and (e) the use of monitoring in an adaptive fashion (Trexler and Busch 2003). However, many of the aforementioned studies begin with an assumption that a classification model has already been identified for the stated goal, or they discuss classification model development only vaguely, by implication, rather than in detail. Our contribution to the above research is to provide a system that can be used with any discrete ecosystem type to develop and test predictive classification models for specific conservation end points, and explicitly incorporate principles from landscape limnology into these freshwater conservation efforts.

A predictive landscape-based classification model analogous to what we describe here was developed to meet the conservation goal of identifying naturally fishless lakes in Maine. Fishless lakes are often poorly identified or sampled, and yet they contain unique and diverse biological communities important for conservation. Schilling and colleagues (2008) developed functional relationships between landscape variables and fish status that led to a simple lake classification model of homogenous states (fish or no fish). The absence of fish in one of the study regions was related to altitude, slope near the lake, and wetland cover within 1000 meters (m) of the lake; in the other region, fish absence was related to the lack of a stream within 50 m of the lake. These functional relationships can then be used as the basis for generating conservation actions targeted at this rare class of freshwater ecosystems using geographic information systems (GIS) databases available for most, if not all, lakes.

The Nature Conservancy's (TNC) hierarchical freshwater classification model for broadscale conservation is another example of the application of a hierarchical, landscape-based classification for the conservation of all water bodies (Higgins et al. 2005). This classification, the overall goal of which is biodiversity conservation, addresses the need for a freshwater classification at both national and international scales, is applicable across broad regions, and uses only data that are readily available from GIS maps. TNC created its classification model—essentially a regionalization framework with an aquatic focus—by clustering the landscape features thought to be most strongly related to freshwater ecosystem biological diversity, principles of fish zoogeography, or professional judgment. In contrast to TNC's classification, our landscape-based classification system does not result in a single overall classification model because we do not make a priori assumptions about which landscape variables most effectively classify water bodies for different purposes. However, in our example application, we used the intermediate spatial scale of TNC's freshwater classification model as one of our predictor variables, and found it important for classifying lake TP and Chl and the relationship between them, but not in the same way for each. Future research should explore further whether and how the incorporation of such regionalization frameworks improves predictive classification models.

Future directions

We have identified two knowledge gaps as priorities for predictive freshwater classification modeling: (1) quantification of the mechanisms behind the relevant hierarchical landscape drivers of ecosystem characteristics; and (2) extension of knowledge from the few well-studied, long-term monitoring sites to the remaining population of ecosystems, for which minimal data exist.

We need to better quantify the mechanisms behind the relevant landscape drivers of freshwater characteristics. As part of developing predictive classification models, we must continue to test hypotheses that consider which landscape features are most important for explaining variation among freshwater ecosystems. In fact, linking landscape patterns to ecosystem processes has been identified as an important research frontier in the broader field of landscape ecology (Turner 2005). Additionally, we need to better understand the relevant spatial scales for measuring landscape variables. For example, the underlying premise when using regionalization frameworks as part of a management or conservation effort is that they capture regional features, unique from subregional features, that affect freshwater ecosystems. To fully understand these inherently hierarchical variables and their effects on freshwater ecosystems, we need to study them in statistically accurate ways. Recent advances in statistical software and multidisciplinary collaborations have provided ecologists with the analytical tools to handle such hierarchical data through the use of multilevel models (e.g., Wagner et al. 2006), to name just one important approach.

Resource constraints often require that decisionmakers approve management strategies based on general knowledge, with only modest information about the systems that will be affected by their decisions. How do we extend the general knowledge obtained from relatively few well-studied systems to ecosystems where information is sparse? As automated environmental sensors and programs that link networks of sensors (e.g., the National Ecological Observatory Network and the Global Lake Ecological Observatory Network) yield increasing and exciting new knowledge (Porter et al. 2009), how do we apply this information to more sites? We need a system for quantitative information transfer from data-rich systems that can be updated with site-specific data from poorly studied systems as those data become available. We propose two possible solutions that are not mutually exclusive. First, a landscape limnology perspective that places well-studied ecosystems into a fully connected landscape mosaic may help managers extrapolate results from well-studied ecosystems to less-studied ecosystems within a similar mosaic. Second, Bayesian inference provides the tools and approaches to robustly integrate different data sources or models (Biggs et al. 2009), as we explain in more detail below.

Without site-specific information regarding the vast majority of freshwater ecosystems, we are initially inclined to think that behavior among poorly studied systems will be similar to that observed in well-studied systems. Yet we know that responses to stressors can be idiosyncratic (Stow et al. 1998). The knowledge derived from well-studied systems can be generally applied to new systems, but this universal application is often insufficient. Using Bayes' theorem, prior information is combined with new data to obtain updated or posterior information. In our nutrient criteria example, prior information pertained to the slope and intercept of the TP-Chl relationship, but more generally it could pertain to the functional form of the TP-Chl model, derived from well-studied lakes. For new lakes without site-specific data (e.g., TP or Chl), we could use readily available GIS landscape data. We would use the CART model to predict the lake TP; we would use the treed model to identify which TP-Chl model is appropriate to predict the lake Chl response to TP. Using one or both of these model predictions, we would hedge our decisions, recognizing uncertainty about the degree to which these relationships represent the new lakes. However, as lake-specific data (e.g., TP values) become available, prior information can be updated with these new observations. This capacity for updating and pooling information (Stow et al. 2009) also makes Bayesian inference an ideal way to implement an adaptive management strategy.

Challenges and opportunities for predictive freshwater classification modeling in a changing world

Freshwater ecosystems are subject to constantly emerging anthropogenic stressors that act at both fine and broad spatial scales and that affect ecosystems in different ways. A system-by-system approach to management was adequate and necessary to deal with point-source pollution during the 20th century, and proved successful for improving the ecological condition of many freshwater ecosystems (Carpenter et al. 1998). The challenges posed by stressors such as invasive species, land use, climate change, and hydrologic modifications are daunting because they are heterogeneous across the landscape and they require an understanding of the spatial patterns of both the stressors and the sensitivity of the receiving water bodies. Approaches similar to the system we present here have been successful for defining the effects of landscape-scale stressors on receiving waters. The acidification of freshwaters is a good example because these pollutants (a) are transported far from sources, (b) influence remote sites, and (c) cross political boundaries, thus posing challenges for management. To address these challenges, researchers identified regions in the United States with potentially sensitive freshwater systems on the basis of acid deposition rates and the important landscape features that determine sensitivity (i.e., geology). Within these sensitive geographical regions, researchers used features such as hydrologic type to classify individual lake sensitivity (Baker et al. 1991). After identifying the lake classes that were most likely to be affected by acid deposition, legislated controls on emissions were set to region-specific targets and the responses of the ecosystems were monitored. The eventual recovery of many of the sensitive lakes provides support for a more conceptual landscape-based system, such as we have presented here.

In addition to the challenges of multiple anthropogenic stressors that are theoretically amenable to mitigation, other stressors, such as climate change, can alter reference targets (i.e., shifting baselines) and public perceptions of what is "typical," and add another layer of complexity to setting goals for ecosystem management and conservation. Ecosystems may experience regime shifts as a result of such complications; the recovery of an ecosystem may follow a different trajectory after removal of the environmental stressor. Given the uncertainty regarding the nature of stressed ecosystem recovery, it is imperative that we improve our understanding of how freshwater ecosystem classes differ in their functional relationships with both natural landscape features and anthropogenic stressors. Improved understanding will better enable identification of systems that are more amenable to management actions and will help managers prioritize scarce resources.

Managing for social values and multiple ecosystem services across the landscape

Management and conservation of freshwater ecosystems is complicated by the diversity of ecosystem services they provide and the differing values that people place on sometimes mutually exclusive services (Rodríguez et al. 2006, Morse et al. 2009). For example, consider that fisheries managers frequently stock nonnative sport fish to enhance angler opportunity. This stocking may conflict with efforts associated with native biodiversity conservation. In this case, classification models developed with the goal of identifying systems that harbor rare or unique biota could be compared with classification models developed to identify lakes in which a sport fishery of nonnatives is most likely to succeed. Spatially explicit knowledge about the conservation and sport-fishing potential of each freshwater ecosystem, combined with knowledge about where people most want to fish for nonnatives (and the attendant economic implications), would lead to comprehensive decisionmaking about how to "trade off" different ecosystem services (and ultimately management goals) across the landscape. A landscape approach that considers when and where different combinations of ecosystem services can be most effectively provided by different ecosystems may be best for addressing this vexing trade-off problem. However, this strategy requires the acknowledgment that every ecosystem cannot provide every ecosystem service. This solution takes a portfolio approach that seeks to maximize ecosystem services provided at the regional scale (i.e., within the population of freshwater ecosystems as a whole) by a sufficient number of individual ecosystems (but not all). Society must deem how many ecosystems are sufficient, considering the values placed on the ecosystem services.

Ultimately, management and conservation outcomes and the associated ecosystem services provided will result from a variety of factors, ideally including the integration of different classification models, their corresponding management and conservation actions, and subsequent effects on the ecosystems. Unfortunately for freshwaters, this integration is hampered because different agencies regulate and address issues of water quality and quantity, physical habitat, fisheries, biodiversity, and endangered species conservation. Although attempts at cross-agency coordination and integration are increasing, such efforts are often limited by a lack of information about the multiple ecosystems under consideration, the lack of a common conceptual framework, and a reluctance to recognize trade-offs in ecosystem services. Our classification system can serve as the scaffolding on which to build different goal-based classification models based on a solid foundation in landscape limnology. These models can serve as the basis for informed interagency discussion about potential conflicts and trade-offs arising from managing multiple systems for multiple ecosystem services and social values, ultimately resulting in improved decisionmaking.

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