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The lake landscape-context framework: linking aquatic connections, terrestrial features and human effects at multiple spatial scales

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Introduction

The principles of landscape ecology provide a powerful means to develop a more robust conceptual understanding of human and hydrogeomorphic controls of lake heterogeneity across space and time (Magnuson & Kratz 2000; Wiens 2002; Kratz et al. 2005). Using a landscape perspective, lakes can be conceptualized as patches (a fundamental unit of a landscape) that are hierarchically organized in a complex terrestrial and aquatic matrix of natural and human-influenced features that interact at multiple spatial scales. Wiens (2002) identified four properties of landscape structure that apply effectively to lakes when treated as patches: (1) *patch quality* describes the physical features of the patch (e.g., lake morphometry, sediment characteristics), (2) *boundaries* mark sharp transitions at patch edges (e.g., lake shorelines), (3) *patch context* describes nearby features (e.g., soils and geology), and (4) *connectivity* defines the degree to which materials and organisms move across the landscape through aquatic connections (e.g. streams, groundwater and wetlands). Because the context for lake patches is hierarchical, a multiscale view that considers both spatial extent (i.e. the size of the study area that contains interacting features, such as lakes, geology, climate, etc.) and spatial grain (i.e. the resolution that features are characterized, such as ecoregion or lake district) is required to link aquatic, terrestrial, and human components into a practical framework.

Such a framework empowers us to more explicitly integrate the myriad of landscape components that we know influence lake ecosystems at different spatial scales and to identify the factors contributing to the spatial structure of variation among lakes.

Existing landscape frameworks have proven to be effective for understanding spatial heterogeneity across lakes (Tonn 1990, Kratz et al. 1997). For example, a combination of biogeographic barriers, abiotic constraints (determined largely by a lake's morphometry and surface water connections) and biotic interactions can help to understand the presence/absence of aquatic species from fish to plants and invertebrates (Tonn 1990; Hershey et al. 1999, Lewis & Magnuson 2000, Hrabik et al. 2005, Rahel 2007). In addition, a lake's position in the regional groundwater and surface flow system (i.e. landscape position) is strongly related to lake water chemistry, clarity, biological measures, and human use of lakes (Kratz et al. 1997, Soranno et al. 1999, Riera et al. 2000, Quinlan et al. 2003, Leavitt et al. 2006, Patoine et al. 2006). Finally, the hydrogeomorphic setting generates large variation among lakes in their response to disturbance (Webster et al. 2000, Cheruvelil 2004).

Despite these examples and calls for a more explicit landscape perspective for lakes (Magnuson & Kratz 2000, Wiens 2002, Kratz et al. 2005), we lack a formalization of these ideas into an integrated conceptual framework that is broadly applicable to a range of lakes and regions. Many existing lake frameworks have been developed for a particular hydrologic setting or omitted humans as important drivers of variation. Interestingly, stream ecologists have a rich history of considering stream ecosystems from landscape perspectives that integrate hydrogeomorphology with ecology (Hynes 1975, Vannote et al. 1980, Frissell et al. 1986, Wiley et al. 1997, Poff 1997). If the valley rules the stream, what rules the lake?

Our goal in this paper is to present the lake-landscape context (LLC) framework. We propose this as a heuristic framework that allows us to understand multiple and interacting natural and human drivers of lake heterogeneity, as well as the relevant spatial scale of interactions among lakes and landscapes. We provide an example of how this framework can be applied at broad spatial scales to partition variance between local and regional spatial scales and end with a discussion of how such a framework will contribute to lake research, conservation, and management.

Key words: lake, landscape-context, landscape position, hydrogeomorphic, disturbance

The lake landscape context (LLC) framework

The LLC framework (Fig. 1) recognizes three sets of landscape features – aquatic, terrestrial and human – that influence lake variation and interact at local to regional

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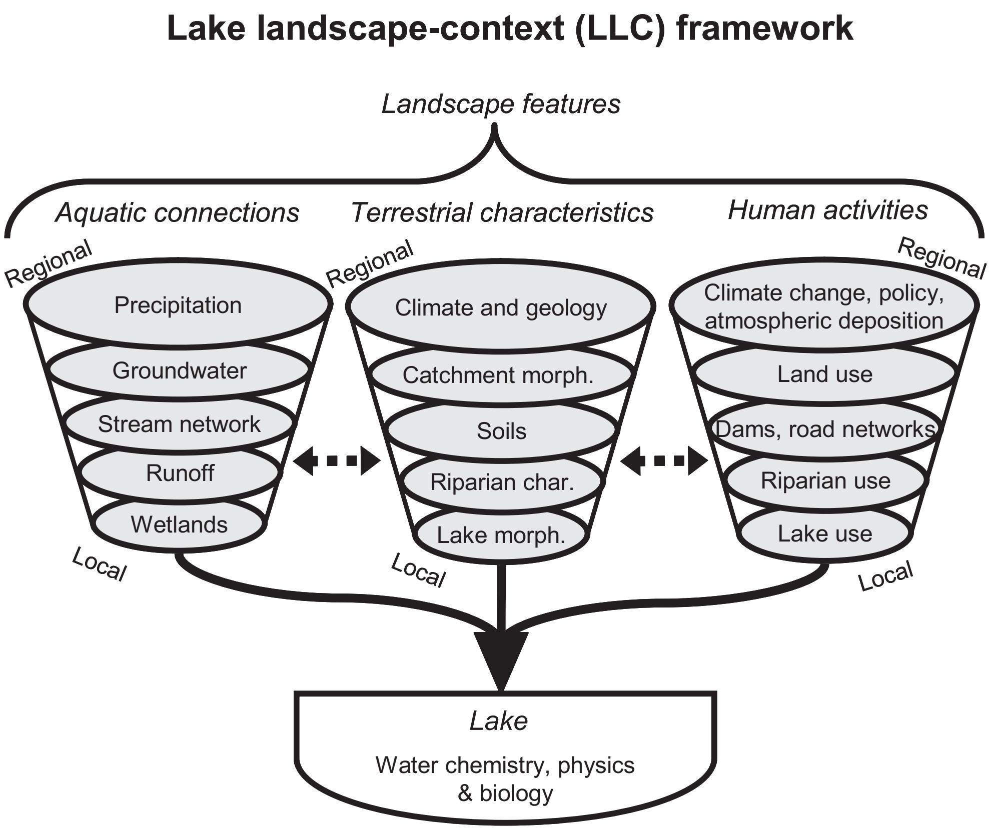

Fig. 1. The lake landscape context (LLC) framework. Each oval represents a relative spatial scale and includes examples of variables that are potentially important in explaining lake limnological variables. The components within the ovals may differ for different limnological variables. Char. is characteristics and morph. is morphometry.

scales. The terrestrial and the aquatic features together define a lake's hydrogeomorphic setting. Each set of features is hierarchically organized, such that regional features both constrain and set the context for local features. Because it is somewhat artificial to separate these three landscape features into their own hierarchical sets, the dashed horizontal lines in Figure 1 illustrate the importance of interactions among the three sets.

Our LLC framework builds on important limnological advances including hierarchical filter models proposed by Tonn (1990), Jackson et al. (2001), and Hershey et al. (1999), in addition to ideas related to landscape position (Kratz et al. 1997) and hydrologic landscapes (Winter 2001). The LLC framework acknowledges this history by integrating terrestrial and aquatic hierarchies and explicitly including human activities, all at multiple spatial scales. However, we also seek to more formally integrate the principles of landscape ecology by treating the structure of the landscape as a patch-corridor-matrix model (Forman 1995) where lakes are treated as patches, and stream and wetland connections are treated as corridors and the human and terrestrial features are treated as the matrix.

We propose that each set of landscape features has a dominant function. Terrestrial features influence the magnitude and composition of materials that are transported from land to water; for example, the type of soils and geology strongly determine the chemical constituents of both groundwater and runoff from land to water (Dillon & Kirchner 1975, Gibson et al. 1995). Aquatic connections determine how effectively these materials and organisms are transported to lakes and the internal processing that occurs within connected aquatic ecosystems (Kling et al. 2000). For example, position in the hydrologic flow system can influence base cation concentrations and diatom communities (Webster et al. 1996, Quinlan et al. 2000), presence of connected wetlands can influence dissolved organic carbon concentrations (Xenopoulos et al. 2004), and surface water connections provide biota refuge from disturbances ranging from winterkill to glaciation (Tonn 1990). Finally, human activities influence both of these dominant functions by adding additional solutes, increasing or blocking the transport of solutes and organisms, and engineering new hydraulic connections. Although each set of landscape features plays its dominant role, each set also performs secondary functions that influence the overall effect of the landscape on lakes. For example, a lake's phosphorus response to forest harvest depends on the lake's position in the groundwater flow system and hydrological connections to wetlands (Devito et al. 2000). We believe this model is broadly applicable because it integrates all features of the landscape rather than a select few.

The spatial structure of lake variation

One important component of our LLC framework is that it is flexible in application across a wide range of spatial extents, defined as the overall size of the study area, from small lake districts to entire continents. To practically apply our framework, an important step is to first quantify the spatial structure of lake variation in order to identify the spatial grain and extent that best captures 'regional' scale variation in landscape features influencing a given lake response.

We examined two lake response variables, total phosphorus (TP) and alkalinity that we expected to have different relationships with landscape features and consequently different spatial structures. We used lake databases from two spatial extents, 478 lakes within a single U.S. state (Michigan; Cheruvelil et al. 2008), and 2316 lakes within a larger spatial extent that included six U.S. states, one of which was Michigan (Wisconsin, Iowa, Michigan, Ohio, New Hampshire and Maine) (Table 1; Authors, unpubl.). For these two spatial extents, we then partitioned lake variation into two spatial scales: 'regional' and 'local'. We defined regions that were assumed to have similar hydrogeomorphic settings within each spatial extent using the Ecological Drainage Unit (EDU) system (Higgins et al. 2005). There are 8 EDU regions within Michigan, and 45 EDU regions within the six-state spatial extent. We partitioned regional and local variation by calculating the intra-class correlation coefficient (ICC) using a one-way ANOVA with random effects (Raudenbush & Bryk 2002, Cheruvelil et al. 2008). This analysis identifies the spatial scale with the highest variation, but does not identify what is causing the variation. However, we can assume that a high ICC reflects high 'regional' variation suggesting that landscape features at broader spatial scales are likely influencing the spatial structure of lake variation; whereas a low ICC reflects variation that is due to local or lake-specific features.

We found that TP and alkalinity had very different spatial variation (Table 1). For TP, the smaller spatial extent (Michigan) had very low regional variation (6%) compared to alkalinity (50 %). This low within-region variation in TP suggests that local landscape variables are more important for determining lake TP than regional variables, a result that is supported by our understanding of catchment and morphometric controls on lake TP. In contrast, for alkalinity, the regional and local variation are about equal, suggesting that regional landscape variables, such as geology and climate, are similar in importance to local variables, such as landscape position, in determining alkalinity.

The structure of spatial variation differs not only for response variable, but also for spatial extent. For both variables, the regional variation of the larger spatial ex-

Table 1. Descriptive statistics of the study areas and the two limnological response variables. Spatial extent is the total area of the study location, spatial grain is the average area of the regions within each spatial extent, and the value in parentheses is the number of regions within each spatial extent. In this example, we use Ecological Drainage Units as the way to delineate the regions. TP is total phosphorus in ug L^{-1}. Alkalinity is in units of mg L^{-1} $CaCO_3$. The ICC is the intra-class correlation coefficient defined as the ratio of among-class (i.e., region) variance to total variance.

	Michigan	6 States*
Descriptive statistics		
Spatial extent (km^2)	147,000	803,000
Spatial grain (km^2)	14,760 (8)	14,560 (45)
TP - *N*	478	2316
TP - Median	13	12
TP - Minimum	3	1
TP - Maximum	155	920
Alkalinity - *N*	475	1970
Alkalinity - Median	106	12
Alkalinity - Minimum	0	–2
Alkalinity - Maximum	225	302
ICC		
TP	6%	58%
Alkalinity	50%	73%

* The six U.S. states are Wisconsin, Iowa, Michigan, Ohio, New Hampshire and Maine

tent (six-states) was higher than the regional variation for the smaller spatial extent (Table 1). These results show that the spatial structure of lake variation is scale-dependent, requiring further investigation at a variety of scales (Cheruvelil et al. 2008). A second important component of spatial scale that needs to be considered is spatial grain. In our example, we have kept the spatial grain constant (i.e. the average size of the regions is the same for both spatial extents). However we know from other studies that spatial grain also matters and warrants further consideration (Cheruvelil et al. 2008).

The role of human activities for understanding regional variation is also dependent upon the lake response examined. Land use/cover is a strong determinant of lake TP, and the six-state spatial extent has a higher proportion of lakes with intense human land use/cover than Michigan does (Soranno, unpubl. data). This difference likely helps explain the relatively high regional variation in lake TP at the six-state extent compared to the low regional variation in TP for Michigan. In contrast, this difference in land use/cover appears to have little effect on variation in alkalinity because alkalinity is less sensitive to human activities and more responsive to geologic features.

In summary, understanding the spatial structure of lake variation is necessary before one can explain the variation due to aquatic, terrestrial and human features at multiple spatial scales. Explaining this variation requires approaches that account for the hierarchical structure of landscape features such as with multi-level models (Cheruvelil 2004, Wagner et al. 2006). The LLC framework provides a framework in which to explore relationships among landscape components and lakes and to seek mechanisms for the observed patterns.

The need for a landscape framework for enhancing lake research, conservation and management

The conceptual underpinning of ecosystem management has a history of focusing on individual and often large ecosystems such as the Colorado River or Lake Michigan. In the past 10–20 years, holistic frameworks for such case studies have been developed to incorporate multiple drivers and stakeholders, and to conduct management in an adaptive way (Gunderson & Holling 2002, Walker et al. 2006). However, few have applied these frameworks to meet the challenges of managing many hundreds or thousands of ecosystems, as is the case for governmental agencies managing large numbers of lakes and streams in their jurisdictions. In fact, many lake-rich regions are managed as if all lakes were the same, despite demonstration that one-size-fits-all policies can erode both ecological and social resilience (Carpenter & Brock 2004). Only by taking a landscape perspective can we begin to understand how to more effectively manage and conserve large numbers of aquatic ecosystems simultaneously rather than on a case-by-case basis. For example, a landscape perspective should help us to set realistic goals for nutrient standards and fishery regulations for lakes of differing hydrogeomorphic starting points (Soranno et al. 2008) and to understand and monitor lakes and their responses to human disturbances.

We propose that our LLC framework provides two important benefits for lake research, conservation and management. First, it helps to focus our attention on the mechanisms underlying observed spatial patterns. Second, it helps us to frame questions related to future or unanticipated environmental problems that face lake ecosystems spanning local, regional, and global scales. Limnologists have addressed many threats to lake ecosystems by effectively considering local scales (e.g., catchment-level features that determine lake eutrophication), to regional scales (e.g., regional patterns in acid deposition and geology that determine lake sensitivity to acid deposition). However, adopting the LLC framework allows us to be better poised to address current and future threats to lakes of globally-relevant stressors such as climate change, invasive species and land cover change. Such issues can only be addressed in a comprehensive fashion by explicitly considering lakes as integrated within a complex mosaic of aquatic connections, terrestrial features and human activities at multiple spatial scales.

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